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# A Comparative Study In Rodent Ethology With Emphasis On Evolution of Social Behavior, I

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## Introduction

The rodents exhibit, as an order, a complex series of morphological, physiological, behavioral, and ecological adaptations. During the long history of adaptive radiation within this order, many instances of convergent or parallel evolution have occurred, thus rendering the subordinal classification quite difficult (Simpson, 1959; Wood, 1955). In spite of such diversity, the rodents form a remarkably unified taxon, and such an example of ecological diversity superimposed on a common morphological theme has intrigued many ethologists concerned with the evolution of behavior. Among the more prominent workers, Dr. I. Eibl-Eibesfeldt has contributed much to our knowledge of the subject and is also responsible for the most recent review of rodent behavior (Eibl-Eibesfeldt, 1958).

Eight years ago the present author initiated a comparative study of rodent behavior, partial results of which have been published in several papers (Eisenberg, 1962a, 1963a, b, c) and abstracts (Eisenberg, 1962b, 1964). These earlier, separate papers do not adequately

reflect the unity behind the undertaking, and in the present paper current results will be combined with previously unpublished data to establish several theoretical principles that have emerged in the course of the work.

Throughout the studies, the behavior patterns have been analyzed in order to determine which movements were stereotyped and, among these, which conformed to the concept of fixed action patterns. Thus, certain behavioral units meeting acceptable criteria could be treated in the same manner as morphological structures and compared from one species to the next in the classical manner developed by Lorenz (1957) and Tinbergen (1951). The ground rules for such comparative studies have been reviewed recently by Wickler (1961) and need not be reiterated here. In my studies, behavioral evolution was approached at the level of discrete behavioral units; such a description of discrete behavioral patterns allowed the formulation of descriptions of more complicated patterns consisting of predictable sequences of discrete units in time. Further analyses of the frequency of occurrence of different stereotyped units of behavior performed in a social context permitted a description of species-specific patterns of social structure. A knowledge of social structure permitted a partial answer to the following question: Do organisms that evolve independently in different geographical locations toward the same ecological niche also evolve similar social organizations? If the answer were yes, then it would be possible not only to predict a social system from a knowledge of niche requirements but also to determine from comparative studies what major environmental adaptations correlated with a given social system. Thus, the comparison of social systems demanded a description of the behavioral units and, in addition, the description of the different forms of social organization by means of some consistent experimental methodology (Eisenberg, 1964). Working in the laboratory with small rodents was possible only when adequate field data were available to correct for any inadvertent misinterpretation brought about by captivity. Finally, methods of quantification had to be developed that permitted a valid comparison among different species. After several years, it became obvious that simple criteria such as the presence or absence of a given behavior pattern would not suffice in determining relevant species differences. Indeed, it appeared that, under the same stimulus conditions, the different species were all capable of exhibiting almost the same discrete units of behavior and, unless major morphological differences interfered, only the different frequencies of occurrence served to separate species. Relative differences rather than absolute differences in behavior became the rule and led the present author to conclusions quite similar to those of Leyhausen (1965).

The study of social organizations ultimately led to an extension of the comparative method. A given type of social organization has a characteristic structure. The structure is the summation of the form and frequency of each type of interaction within an interacting group. Thus, the social structure reflects the mechanisms of interaction and the adaptive role of the interaction patterns determines the selective advantage of the system at the level of the individual member. On the other hand, a set of complementary emergent properties results when one considers that the social structure itself reflects an adaptation to a given set of environmental relationships that are reflected in the physiology or metabolism of the social group taken as a whole.

Future research on the adaptive nature of whole societies will necessarily have to concern itself with biologically viable societies, i.e., a social unit or series of social units that are maintaining their numbers over long periods of time. In essence, then, conclusions concerning the adaptive nature of groups must be based on groups exhibiting a prevailing reproductive success.

The interrelationships of the various measurable phenomena exhibited at the level of the individual and the group are presented in figure 1.

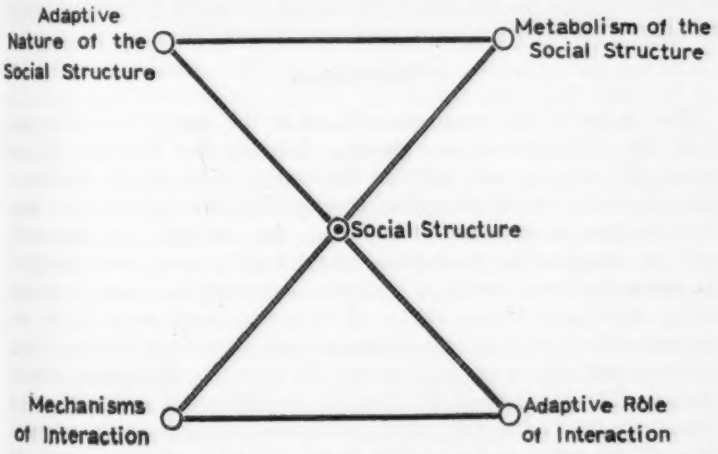
Adaptive Nature of the Social Structure
Metabolism of the Social Structure
Social Structure
Mechanisms of Interaction
Adaptive Rôle of Interaction

FIGURE 1.—Diagram indicating two possible levels of analysis commonly applied to social structures.

The present report thus demonstrates a method for the analysis of mammalian social structure, the application of the methods to several families showing varying degrees of convergence or parallelism, the reformulation of the term "species-specific behavior," and a discussion of social evolution within the Rodentia.

In a comparative study that spans 3 families and 34 species from three continents, the problems of acquisition and maintenance are of paramount importance. I should like to acknowledge the efforts of my laboratory assistant, Mr. David Williams, who lent his sensitive talents wholeheartedly to the work before us in Vancouver. Specimen donations were also an integral part of this study. I am indebted to Dr. D. Birkenholz of Illinois State University for 3 *Heteromys desmarestianus;* to Mrs. W. Downs of Yale University for 3 *Gerbillus gerbillus,* 2 *Jaculus jaculus,* and 2 *Jaculus orientalis;* to Dr. T. Reed, Director of the National Zoological Park, for 1 *Pachyuromys duprasi;* and to Mr. W. Preston of the University of British Columbia for 12 *Perognathus parvus.* In addition, I should like to cite Mr. Ralph Curtis of Miami, Fla., who was instrumental in arranging the importation of a series of rodents from Pakistan that formed the basis for our dipodid and gerbilline comparisons.

The studies reported on in this paper were financed in part by the following grants: E 350 and A 1371 from the National Research Council of Canada, and a general research board grant from the University of Maryland. The author is indebted to the Departments of Zoology at the University of California, Berkeley, the University of British Columbia, and the University of Maryland for the space and facilities utilized in the 7-year course of this study.

## The Subjects

The choice of the specimens utilized in this study was influenced both by circumstances and design. Initially the behavior of one genus, *Peromyscus,* was selected for study. This North American group includes over 40 recognized species (Hall and Kelson, 1959) that have adapted to a myriad of habitats. As a genus it has lent itself well to comparative ecological, physiological, and morphological studies and offers a wealth of background studies that may be drawn on by ethologists (King, 1967). Four species were selected by the present author for behavioral studies, including two from the Transition life zone and two from the Sonoran life zone (see Eisenberg, 1962a, 1963a). The behavior of this group is the subject of a recent review (Eisenberg, 1967) and will not be redescribed here; however, relevant data will be introduced since this group of four species represents an example of the range of behavioral variation within one genus.

Several questions were raised in the course of the *Peromyscus* study concerning species-specific changes in social behavior resulting from adaptation to desert habitats. For this reason a complete rodent family, the Heteromyidae, was studied in order to correlate generic differences with niche requirements as I compared moist forest-adapted genera (e.g., *Heteromys* and *Liomys*) with desert or semidesert-

adapted genera, *Perognathus*, *Microdipodops*, and *Dipodomys* (Eisenberg, 1963b). The results combined with the *Peromyscus* data suggested that any limiting factors a desert environment may impose concerning space requirements of a given individual rodent are not necessarily limiting with respect to the particular species-specific form of the social organization.

To confirm this hypothesis, two Old World taxa of desert-adapted rodents were studied, the Gerbillinae and the Dipodidae. Table 1 contains a list of the specimens included in this study with their geographical origins. Exact capture localities for specimens trapped by the author are included in previous publications (Eisenberg, 1962a, 1963a, b).

Adaptation to an arid environment involves the solution of several severe physical problems including (1) lack of water, (2) widely spaced food plants with concomitant loss of cover, (3) extremes of heat and cold. The behavioral, morphological, and physiological solutions to these problems are varied when the vertebrates are surveyed as a group (Schmidt-Nielsen, 1964), but all mechanisms are geared to the same ends: maintenance of a constant body temperature (at least during active periods), conservation of body fluids, and procurement of sufficient food. A number of small desert rodents have adapted in a similar fashion, providing typical instances of parallel physiological or behavioral evolution. For example, some species of the gerbilline, dipodid, and heteromyid rodents can recover metabolic water in the kidney and live on dry foods alone (Burns, 1956; Kirmiz, 1962; Schmidt-Nielsen, 1964). Furthermore, many desert rodents are nocturnal, construct burrows that are plugged during the day, and cache quantities of food. In several cases bipedal locomotion has evolved (e.g., within the Heteromyidae and the Dipodidae).

None of these behavioral attributes is confined to desert-dwelling species, but the total complex of attributes is unique to a certain type of desert-dwelling form (Eisenberg, 1963b). Within the genus *Peromyscus*, desert adaptation has taken place without the evolution of either bipedality or the ability to reuse metabolic water. The family Heteromyidae exhibits a range of morphological adaptations to a desert environment wherein only the genera *Microdipodops* and *Dipodomys* culminate their evolution with both an extremely specialized gross morphology and the ability to live on metabolic water alone (Eisenberg, 1963b).

Confronted with such a range of adaptations to the same set of problems in the desert, any correlation between behavior and ecology must take cognizance of the multiplicity of variables affecting the overall adaptation pattern. For this reason, tables 2 through 5 summarize the major similarities and divergences regarding reproduc-

tion, morphology, habitat, and ecology. Ecological data for the Gerbillinae and Dipodidae are adapted from Ognev (1963), Petter (1961), Zahavi and Wahrman (1957), and Kirchshofer (1958). Figure 2 compares the overall phylogeny for the three major families studied; it is derived from the work of Ognev (1963), Herold and Niethammer (1963), and Wood (1935).

The desert-adapted species show wide divergences when reproduction, maturation rates, morphology, and ecology are compared. The jerboas differ from the kangaroo rats in that some genera of jerboas hibernate and the maturation of the young is prolonged. On the other hand, the dipodids and the genus *Dipodomys* show a close parallel in their morphology and habitat requirements. Certainly the closest correspondence between rodent families occurs when some species of gerbil (i.e., *Gerbillus nanus*) are compared with the heteromyid species of the genus *Perognathus*. In any event, tables 2 through 5 emphasize the differences that may have a bearing on divergences in the form of social organizations (see p. 31).

## Methodology

When not under direct observation, the subjects were held as individuals or pairs in glass-sided cages with wire tops and wooden floors. These holding cages were of two general sizes containing floor areas of 90 to 180 square inches. The animals were fed a mixture of sunflower seeds, commercial rat pellets, rolled oats, millet, and fresh lettuce (see also table 1).

The analysis of behavior began with a description of the discrete units that comprise the total repertoire of activity patterns displayed by the subject under study. In order to give the animal ample opportunity to display the full range of its behavior patterns, simulated natural habitat cages were employed. Such cages contained artificial burrows; they are fully described in a previous publication (Eisenberg, 1963b, p. 5). In the present study, the floor areas of the burrow cages included three sizes: 864, 550, and 360 square inches. Nocturnal forms were observed by a red light during their normal dark cycle of activity. Once the behavioral units had been described, the subjects were exposed to several testing situations that may be treated under two headings: (1) behavior patterns of the solitary animal and (2) patterns of social behavior.

The behavior patterns displayed by the isolated animal fall under the general categories of exploratory and maintenance behavior. In order to analyze the differences among species, standard tests were run by allowing an animal to move freely in a glass-fronted arena containing specific artifacts such as stones, hay, a tree branch, and a small amount of food. The arena sizes included floor areas of 748,

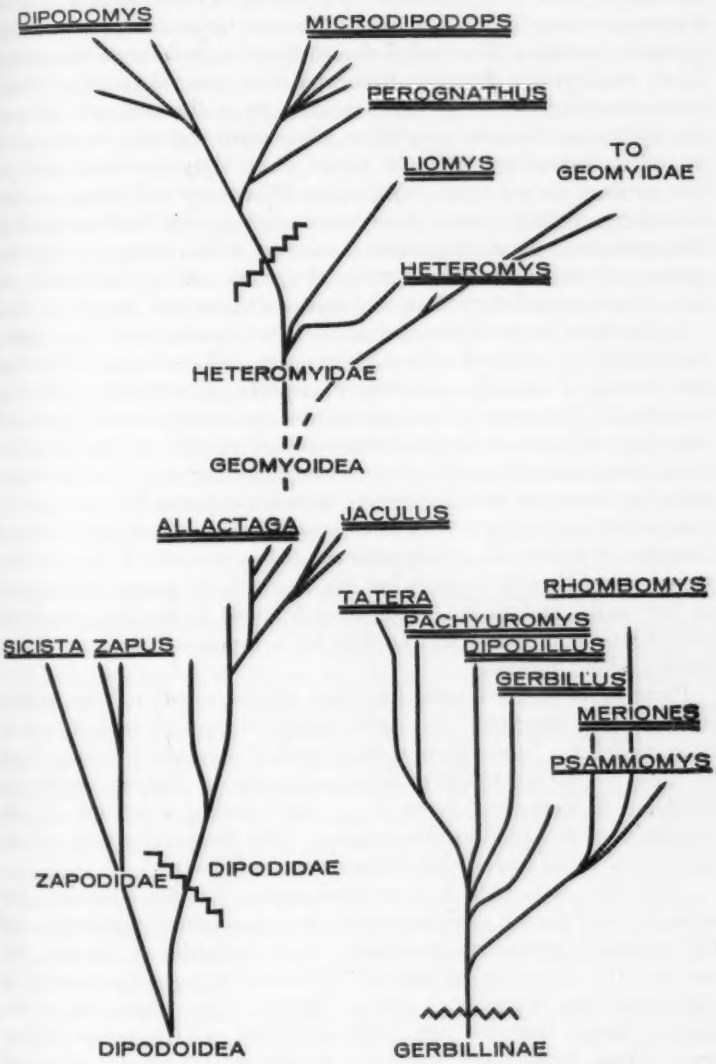


FIGURE 2.—Inter-relationships of major genera from three families of desert-adapted rodents (double underline=all genera included in present study; genera above jagged line are commonly found in arid or semi-arid habitats).

1598, and 2304 square inches. Employing a tape recorder, the behavior was described in a semicoded fashion by an observer concealed behind a screen. The verbal descriptions on tape were transcribed later, employing a constant 10-second time interval to allow further for a consideration of the temporal changes in the behavior patterns. An operations recorder coupled to a keyboard was also employed for recording behavioral units in time. Both data-recording methods are outlined in previous publications (Eisenberg and Kuehn, 1966; Eisenberg, 1963b). Such data were analyzed by various methods that permitted an accurate determination of the changes in the frequency of responses, the duration of specific activity patterns, and the frequency and durational changes over extended periods of time.

A problem in quantification arose in comparing acts that had a brief duration, coupled with a clear onset and cessation, with those acts having a variable duration of imperfectly definable onset and cessation. The more or less brief actions generally were counted and described in terms of straight numbers per unit time. On the other hand, such activities as driving, chasing, fighting, etc., were recorded either in terms of actual duration or were counted for a frequency analysis by employing a 10-second time criterion. Such acts having a duration of 10 seconds or less were treated as one unit; if the duration were greater than 10 seconds but less than 20, the action was treated as two units, and so on. Indication is made in the text whenever the 10-second criterion was applied for a frequency analysis of acts having a long duration.

Patterns of social interaction were also recorded by the general methods just described—by verbal means on tape or with an operations recorder. In addition, a third method involved a weekly check of cages containing freely growing populations. Pairing tendencies, incidence of wounding, litters born, and breeding condition of individuals were censused in this manner. The three approaches to the analysis of social interaction patterns are as follows:

(1) The encounter in a neutral arena: In this situation, two animals were placed simultaneously in a standard environment and the resultant interaction recorded. Such variables as the sex, the age, and the physiological state of the encountering animals could be controlled (see Eisenberg, 1962a, 1963b). The glass-fronted encounter arenas included 748, 1598, and 2304 square inches of floor area. Data from such standard encounter situations permitted species comparisons with respect to differences in the frequency and duration of various social behavior patterns.

(2) The territorial encounter: This was a variant of the simultaneous encounter technique and involved the use of a cage divided into two or three equal compartments as described previously (Eisen-

berg, 1963b, p. 4). The encounter boxes included 1110, 1728, and 1950 square inches of floor area. Utilizing this technique, some measure of the influence of the locus on the outcome of an encounter could be assessed.

(3) The formation of social groups: In this situation pairs or groups were allowed to remain together as a result of either a simultaneous or a territorial encounter. Several measurements were recorded, including the tendency to nest together, the incidence of wounding, the tolerance of the male by a female during parturition and rearing, the effect of the male on the female's estrous condition, and the effect of the adults on the survival, growth, and development of the young. Various cage sizes were employed in the study of the pairing tendencies and the social tolerance during the growth of confined populations. These included cages with floor areas of 180, 328, 550, 864, 1110, 1728, 1950, 2304, 5040, and 6480 square inches. Studies of this nature yielded information concerning species-specific differences in social tolerance. Pair tolerance and the growth of confined populations varied from species to species; the solitary species required a large space coupled with a complex environment in order to reproduce successfully.

## Terminology

As the initial analyses progressed, it was found that the behavioral repertoires of the different species were remarkably similar in their gross form. The social behavior of small nocturnal mammals appears to include a reliance on auditory, tactile, and chemical communication, with a reduced role for visual communication. Hence, the evolution of complex movement patterns with concomitant morphological changes that are employed in the visual display of many diurnal vertebrates such as birds, lizards, and certain fishes are reduced in the present group. The role of chemical and auditory signals in the nocturnal rodents is still poorly known and, in the present study, the behavioral units were recorded without direct reference to their communicatory function. As a result, the behavioral inventories show more uniformity than might be expected by students of avian or fish behavior. This uniformity permitted a single list of defined behavioral elements to serve for all species.

Complete ethograms exist for the heteromyid rodents (Eisenberg, 1963b), the genus *Peromyscus* (Eisenberg, 1962a, 1963a, 1967), *Meriones persicus* (Eibl-Eibesfeldt, 1951), and *Gerbillus nanus* (Kirchshofer, 1958); in addition, ontogenetic data exist for *Meriones tamariscinus* (Rauch, 1957) and a behavior study of the jerboa is near completion by Hackinger (pers. comm.).

Rather interesting data on the reproductive behavior of *Pachyuromys duprassi* and other gerbillines are contained in the early work

of Lataste (1887). Since the species of *Meriones* and *Gerbillus* included in this study resemble in their behavior the species cited previously, no attempt is made here to include an exhaustive ethogram for them.

The list below includes all behavioral terms utilized in the current study. The list serves for all species although not every species includes all of the behavior patterns in its behavioral inventory. The complete descriptions of these behavioral elements and their functional organization are included in Eisenberg (1962a, 1963b), Eibl-Eibesfeldt (1951, 1958), and Kirchshofer (1958). Both German and English equivalents are presented to avoid terminological confusion.

The postures and movements listed here represent two types of classification. Some of the terms apply to discrete muscular movements consisting of an orientation movement, a stereotyped component, or a fusion of both. Other terms are descriptive in that they indicate a functional unit of motor patterns. Convenience has dictated this mixed presentation. Please note that the functional units described here may well be analogous units when two or more species are compared. It is not intended that the equivalence of terms should necessarily imply homologous motor units.

| Eisenberg | Eibl-Eibesfeldt |
|---|---|
| General Maintenance Behavior | |
| Sleeping and resting | Schlafen und Rasten |
| Curled | Zusammengerollt |
| Stretched | Ausgestreckt |
| On ventrum | Bauchlage |
| On back | Rückenlage |
| Sitting | Sitzen |
| Locomotion | Fortbewegung |
| On plane surface | An der Boden |
| Diagonal | Kreuzgang; Laufen |
| Quadrupedal saltation | Hoppeln; Galopieren |
| Bipedal walk | Bipedes Schreiten |
| Bipedal saltation | Bipedes Springen |
| Jumping | Springen |
| Climbing | Klettern |
| Diagonal coordination | Klettern im Kreuzgang |
| Fore and hind limb alternation | Stammklettern |
| Swimming | Schwimmen |
| Care of the body surface and comfort movements | Körperpflege |
| Washing | Putzen |
| Mouthing the fur | Fellpflege |
| Licking | Belecken |
| Nibble | Beknabbern |
| Wiping with the forepaws | Putzen mit den Vorderbeinen |
| Nibbling the toenails | Nägelputzen |
| Scratching | Sich-Kratzen |
| Sneezing | Niesen |

| Eisenberg | Eibl-Eibesfeldt |
|---|---|
| **General Maintenance Behavior—Continued** | |
| Care of the body surface and comfort movements—Continued | |
| Cough | Husten |
| Sandbathing | Sandbaden |
| Ventrum rub | Bauchreiben |
| Side rub | Flankenreiben |
| Rolling over on the back | Wurfen auf den Rücken |
| Writhing | Schlängelbewegungen |
| Stretch | Sich-Strecken |
| Yawn | Gähnen |
| Shake | Sich-Schütteln |
| Defecation | Koten |
| Urination | Harnen |
| Marking | Markierung; Duftmarkierung |
| Perineal drag | Rutschen auf der Anal region |
| Ventral rub | Bauchreiben |
| Side rub | Flankenreiben |
| Ingestion | |
| Manipulation with forepaws | Futterhalten |
| Drinking (lapping) | Trinken (Lecken) |
| Gnawing (with incisors) | Nagen |
| Chewing (with molars) | Kauen |
| Swallowing | Schlucken |
| Holding with the forepaws | Handhaben |
| Gathering foodstuffs and caching | Sammeln |
| Sifting | Prüfen |
| Dragging, carrying | Eintragen |
| Picking up | Aufheben |
| Forepaws | mit dem Pfoten |
| Mouth | mit dem Maul |
| Hauling in | Einholen |
| Chopping with incisors | Häckseln |
| Digging | Graben; Lochgraben |
| Placing | Ablegen |
| Pushing with forepaws | Nachstopfen |
| Pushing with nose | Schnauzen-stossen |
| Covering | Zugraben |
| Push | Zuscharren |
| Pat | Festdrücken |
| Digging | Graben |
| Forepaw movements | Scharren |
| Kick back | Auswerfen |
| Turn and push (forepaws and breast) | Hinausschieben |
| Turn and push (nose) | Hebeln |
| Nest Building | Nest bauen |
| Gathering | Aufsammeln |
| Stripping | Zerspliesen |
| Biting | Beissen |
| Jerking | Hockreissen (des Kopfes) |

| Eisenberg | Eibl-Eibesfeldt |
|---|---|
| **General Maintenance Behavior—Continued** | |
| Nest Building—Continued | |
| Stripping—Continued | |
| Holding | Halten |
| Pushing and patting | Andrüken der Pfoten |
| Combing | Abstreifen |
| Molding | Ausmulden |
| Depositing | Ablegen |
| Isolated animal exploring | Einzel Tiere |
| Elongate, investigatory | Erkünden mit Fluchtmotivation |
| Upright | Aufrichten; Männchenstellung |
| Testing the air | Winden |
| Rigid upright | Sichern |
| Freeze (on all fours) | Erstarren |
| Escape leap | Flucht-springen |
| Sniffing the substrate | Spüren |
| Whiskering | Vibrissenzucken |
| **Social Behavior** | |
| Initial contact and contact promoting | Kontaktaufnahme |
| Naso-nasal | Nase an Nase; Schnauzen Kontrolle |
| Naso-anal | Beschnuppern des Ano-Genital Region |
| Grooming | Soziale Hautflege |
| Head over–head under | Kopfunterschieben |
| Crawling under and over | Überkriechen und Unterkriechen |
| Circling (mutual naso-anal) | Beschnuppern im Kreisgang; Kreisen |
| Sexual | Sexual |
| Follow and driving | Treiben |
| Male patterns | Männliche Verhaltensweisen |
| Mount | Aufreiten |
| Gripping with forelimbs | Stimulieren |
| Attempted mount | Aufreitversuch |
| Copulation | Kopulation; Paarung |
| Thrust | Friktionsbewegungen |
| Intromission | Einführung |
| Ejaculate | Ejakulierens |
| Female patterns | Weibliche Verhaltensweisen |
| Raising tail | Präsentieren |
| Lordosis | Paarungstellung |
| Neck grip | Nackenbiss |
| Postcopulatory wash | Sich-putzen |
| Approach | Annährung |
| Slow approach | Vorsichtige Annährung |
| Turn toward | Zuwendung |
| Elongate | Erkünden mit Fluchtmotivation |
| Agonistic | Flucht, Angriff, u.s.w. |
| Threat (proper) (remains on all four legs) | Drohen |

| Eisenberg | Eibl-Eibesfeldt |
|---|---|
| **Social Behavior—Continued** | |
| Agonistic—Continued | |
| Rush | Angriff |
| Flight | Flüchten |
| Chase | Verfolgen |
| Turn away | Abwenden |
| Move away | Weggehen |
| Bite | Kampfbeissen |
| Locked fighting (mutual) | Kampfstellung |
| Fight (single) | Kampfstellung |
| Defense (on back) | Abwehrstellung |
| Side display | Breitseitsdrohen |
| Shouldering | Schieben |
| Sidling | Drücken mit der Körperseite |
| Rumping | Schieben |
| Uprights | Aufrichten |
| Class I (upright threat) | Drohstellung |
| Class II | Drohabwehr |
| Locked upright | |
| Striking, warding | Pfotenschlagen |
| Sparring | Pfottentrommeln (Kampfvorspiel) |
| Tail flagging | |
| Kicking | Treten |
| Attack leap | Anspringen |
| Escape leap | Flüchtspringen |
| Submission posture | Demutstellung |
| Defeat posture | Aufgebenstellung |
| Tooth chatter | Zahnwetzen |
| Drumming | Trommeln |
| Pattering (with forepaws) | Pfotentrommeln |
| Tail rattle | Schwanzzittern |
| Miscellaneous patterns seen in a social context | |
| Sandbathing | Sandbaden |
| Digging and kick back | Scharren und Auswerfen |
| Marking | Markieren |
| Ventral rub | Bachreiben |
| Side rub | Flankenreiben |
| Perineal drag | Rutschen auf der Anal region |
| Pilo-erection | Fellsträuben |
| Trembling | Zittern |

## Behavior Patterns of the Solitary Animal

LOCOMOTION.—When a series of genera or species are compared, the presence or absence of a behavior pattern is often correlated with a corresponding presence or absence of some morphological feature. This is nowhere better illustrated than with bipedal locomotion. As discussed by Howell (1932), Hatt (1932), and Ognev (1959), bipedal, saltating locomotion occurs when a set of morphological features are

present, including modifications in the musculature and vertebral column, reduction in the number of hind toes, lengthening of the hind feet, shortening of the forelimbs, fusion of the cervical vertebrae, and modifications of the tail. To be sure, most rodents possess the ability to stand on their hind legs and walk or even hop for a short distance, but sustained bipedal saltation does not occur as a normal behavior pattern with the absence of certain morphological and physiological correlates. In the group under study, full bipedal locomotion was exhibited only by *Microdipodops*, *Dipodomys*, *Allactaga*, and *Jaculus*. The latter two genera are more advanced in that the first and fifth toes are reduced (*Allactaga*) or absent (*Jaculus*) and in both forms the metatarsals are fused to form a "cannon bone."

COMFORT MOVEMENTS.—Sandbathing: Sandbathing is a complex movement pattern functional in dressing the pelage. It is composed of several distinct behavioral units, including side rubbing, ventrum rubbing, writhing from side to side, and rolling on the back. All these units are part of the total behavioral inventory of most rodents and other mammals; however, the organization of these units into a specific pelage-dressing pattern tends to be taxon-specific (Eisenberg, 1963c). The species-typical movement complex termed "sandbathing" is a normal part of the behavioral repertoire in most rodents that have adapted to arid habitats. It should be understood that sandbathing is not confined to desert rodents alone, but that the frequency of occurrence and stimuli necessary to elicit the pattern are characteristic of desert-adapted species. In the current study, *Gerbillus gerbillus*, *G. nanus*, *Tatera indica*, *Meriones unguiculatus*, *M. hurrianae*, *Pachyuromys duprassi*, *Allactaga elator*, *Jaculus jaculus*, *J. orientalis*, *Peromyscus crinitus*, and all species of *Microdipodops*, *Perognathus*, and *Dipodomys* exhibited functional sandbathing. Dressing the pelage by rolling or rubbing in dry soil may be accomplished potentially by any of the several discrete movements mentioned above. Typically the animals exhibit digging movements with the forepaws and the kicking back of accumulated earth with the hind limbs. Digging movements serve to dust the fur of the ventrum and often, while digging, the animal may exhibit slight forward extensions of the body as it presses its ventrum against the substrate. The components following digging and kick back are classified as a side rub, ventral rub, or rolling over, but this tripartite classification masks some subtle details. Since the side rub and ventral rub commonly occurred in the series of rodents studied, I include a brief description of the variations:

The side rub: This may involve lowering the head to the substrate and sliding forward on the side while first extending and then flexing the torso. The action may be swift with only a slight exten-

sion and flexion of the body, or it may involve a movement of both hind legs forward as the torso flexes. During the extension phase, the chin may rest flat on the substrate with the result that the chest is rubbed in the sand. The latter twisting is especially common in the dipodids studied.

The ventrum rub: In this study, the ventrum rub was defined arbitrarily as extension and flexion of the body axis with the ventrum pressed against the substrate. Typically the hind feet are thrust forward even with or beyond either side of the head during the flexion phase. The ventrum and perineal region are thoroughly scrubbed into the substrate. It can be seen from this description that digging and the side rub, plus the twisting of the body, will suffice to dust the entire pelage with soil. The ventrum rub is not always necessary as a pelage dressing component.

Rolling on the back while writhing from side to side was rarely shown by the species studied although it was observed occasionally with *Tatera indica*, *Meriones unguiculatus*, and *Pachyuromys duprassi*.

The frequency of side rubs to ventrum rubs varies in a species-specific manner. Table 6 indicates the trends for seven species from three families. The sandbathing Heteromyidae display a range of ventrum rubbing from 23 to 45 percent, whereas the dipodid *Allactaga* displayed only 8 percent ventrum rubs and the gerbils *Meriones* and *Gerbillus* displayed virtually no ventral rubbing as a component of sandbathing. The discrete components of sandbathing occur in sequences and each single event may be followed by a second event within an interval range of one-half to an unknown number of seconds exceeding 500. The frequency distributions for intervals separating sandbathing acts were plotted. Since the majority of intervals fell within 3½ seconds, this interval was selected arbitrarily as the limiting interval separating acts within the same sequence. For each species, all sequential acts were plotted in a Latin square in a manner described previously (Eisenberg, 1963c). Table 7 portrays the results, which give an indication of how the components of sandbathing are integrated. *Meriones* and *Gerbillus* are prone to alternate side rubs from one side to the other. *Allactaga* seems equally prone to alternate or rub the same side a second time. *Dipodomys deserti*, *Perognathus californicus*, and *P. parvus* tend to alternate sides whereas *D. nitratoides* shows a preference for rubbing the same side. All the Heteromyidae integrate ventrum rubs with side rubs into a functional sequence.

All species exhibit locus specificity in their sandbathing on consecutive days. There is also a pronounced tendency in some species to sandbathe at the locus of a partner during a social encounter (see p. 22). The occurrence of locus specificity and the exchange of loci

during an encounter implies that chemical communication is taking place; thus, the functional classification of sandbathing really includes a marking function as well. In addition to the movements involved in dressing the pelage, these animals may have definite marking movements.

Marking: Marking is a functional term including several behavioral units. From a functional standpoint a marking pattern serves to spread some chemical substance at a specific locus. Such a chemical presumably has communicatory value. Many rodents utilize a marking pattern that involves a depression of the anal-genital region in order to bring these glandular areas into contact with the substrate as the animal moves about in its living space. This is termed the perineal drag. Urine and feces may serve as chemical markers in addition to glandular exudates. When special glandular areas are concentrated on other parts of the body such as the flanks or ventrum, side rubbing or ventrum rubbing may be expressed as a marking movement. The perineal drag is a movement common to all the rodent species studied. Ventrum rubbing is a ritualized marking movement shown by the genus *Meriones*. The latter genus is characterized also by a large gland-field in the ventral epidermis.

It should be noted that sandbathing can serve the dual function of dressing the pelage and marking (Eisenberg, 1963b, c); thus, in desert-adapted species the sandbathing behavior tends to be concentrated at a specific locus and can serve as a focus of activity for two or more interacting individuals.

Washing: Washing (autogrooming) is displayed in a typical myomorph fashion (Bürger, 1959). The chief modifications in movement pattern are the results of morphological modifications. Hence, the short forelimbs and short necks of the bipedal genera restrict the movement of the head in the vertical plane and necessitate a rotation of the head when it is washed with the forepaws.

Burrow construction.—The desert-adapted rodents of the families Cricetidae, Dipodidae, and Heteromyidae construct extensive burrow systems that employ basic digging patterns involving the forepaws and hind limbs (Eisenberg, 1963b). The teeth may be used to gnaw into a hard substrate; *Allactaga elator* is most prone to gnaw when constructing burrows. This behavioral trait is reflected in the protruding dentition, which enables *A. elator* to gnaw into a flat surface without a crack or crevice that would permit a starting point for gnawing.

Burrow walls are packed by a pushing and patting motion of the forepaws (Eisenberg, 1963b). This movement pattern is typical for many rodent species, and the nose and incisors may also be involved in packing loose soil. *Tatera* and *Meriones*, when packing, employ the

forepaws and nose by jerking the body back and forth in the vertical plane while holding the forepaws rigid on either side of the nose. The forepaws and nose strike the soil and serve to tamp it firmly into place. *Allactaga* and *Jaculus* pack loose soil by raising and lowering the head in the vertical plane, thus repeatedly bringing the snout and incisors against the substrate. This packing method appears to be highly ritualized in the Dipodidae. The heteromyid rodents as well as *Gerbillus* and *Pachyuromys* appear to employ pushing and patting with the forepaws as the principal method for packing the tunnel walls.

ASSEMBLY OF FOODSTUFFS.—Studies of *Meriones persicus* (Eibl-Eibesfeldt, 1951) indicate a tendency to bite pieces of food (e.g., vegetable matter, stalks, roots, pods) into small pieces, which are then cached. This behavior pattern has been termed "Häckseln" and is here translated as chopping. *M. unguiculatus*, *M. hurrianae*, and *Tatera indica* all exhibited this trait.

The caching of foodstuffs either in the burrow or in discrete loci within the animal's home range is a behavioral trait shared by many species of rodents. The family Heteromyidae is characterized by a persistent tendency to gather and cache great quantities of grain, and this behavioral trait is correlated with the possession of capacious, externally opening, fur-lined cheekpouches (Eisenberg, 1963b). None of the other genera in the current study exhibited such persistent caching behavior, and the dipodid genera do not seem to cache very much at any time during their annual cycle. *Allactaga* and *Jaculus* will assemble dried grasses in their burrows, but this material is generally used in nest building rather than as food (see table 8).

DISCUSSION.—Behavioral and ecological convergences appear to be very close when the genera *Perognathus*, *Gerbillus*, and *Pachyuromys* are compared. Although the genera *Microdipodops*, *Dipodomys*, *Jaculus*, and *Allactaga* are ecologically similar and have evolved a similar morphology correlating with their bipedal form of locomotion, rather profound behavioral and physiological differences separate the bipedal Heteromyidae from the Dipodidae. The most basic correlate appears to involve the reduced caching tendency of *Jaculus* and *Allactaga* with a concomitant tendency to hibernate or exhibit periods of torpor (Skvortsov, 1955, 1964). *Dipodomys* caches seeds and is not known to hibernate.

Since the Heteromyidae are essentially solitary rodents with a very low threshold for the exhibition of agonistic behavior, this tendency toward asocial behavior may correlate with the fact that the genera *Dipodomys* and *Microdipodops* do cache and the fact that the selective advantage of caching is related to a dispersed or solitary social structure.

Sandbathing is a trait shared by all desert-adapted rodents. It would appear that increased sebaceous secretion is a necessary condition to reduce evaporative water loss through the epidermis. In addition, many desert rodents have a dense pelage with a concomitant increase in sebaceous glands as an adaptation to extremes of cold during the desert night (Sokolov, 1962). With the increase in sebaceous glands and secretion, one finds a corresponding necessity to dress the pelage. Since all species of rodents studied appear to dry their fur when it is moistened by means of either extending and flexing the body while lying on their side or ventrum or rolling over, the conclusion is unavoidable that ritualized sandbathing has evolved from the same set of basic movements in all rodent families. It is interesting to note that selection has favored a relatively stereotyped pattern that varies in a species-specific manner (see table 7). The higher taxonomic categories show less uniformity; however, the sandbathing Heteromyidae are remarkably uniform with their tendency to integrate side rubs and ventral rubs. This characteristic tends to set off the Heteromyidae from the Gerbillinae and Dipodidae.

Since sandbathing has the dual function of dressing the pelage and leaving a chemical trace of presumptive communicatory value, the evolutionary origins of sandbathing are inextricably tied to marking. Marking by means of the perineal drag probably had its origin in a common cleaning movement that consisted of wiping the anal-genital area on the substrate after urination or defecation. The stretch involving extension and flexion of the body also frequently accompanies elimination after the animal has awakened from prolonged sleep. Thus, selection could favor a combined ventral rub with perineal drag as a marking movement if the sebaceous secretions of the ventral epidermis had some inherent communicatory function that affected reproductive success or survival of the genotype. Such a ritualized marking pattern appears to have arisen as an independent element in *Meriones*, whereas in the Heteromyidae the ventral rubbing with its marking function has been combined with side rubbing in a functional sandbathing sequence (see table 9).

### Patterns of Social Behavior

In a recent review of rodent social behavior (Eisenberg, 1966), I attempted to outline the origins and evolution of the various social systems to be found within the Rodentia. Social systems may be classified into two categories: solitary and communal. The communal systems have several subtypes including monogamous, polygamous, and family band groupings. For convenience, I will restrict the discussion in this paper to three categories: solitary, pair tolerance, and communal. The latter category corresponds to the family band

as defined in the previously quoted monograph. It is the central thesis of this section that a given species has a typical social organization that falls into one of the three major categories.

In order to describe quantitative differences among species, three techniques have been employed: (1) the simultaneous or territorial encounter; (2) the maintenance of pairs through parturition; and (3) the study of groups derived from internal recruitment by births (see p. 26). The species-specific social organization is a result of species differences in the ability to tolerate contact with conspecifics. Thus, each species has a social tolerance that, when exceeded, will result in pathologies such as failure of the female estrus cycle, abandoning or destroying the litter by the mother, delayed maturation of the young, fighting to the point of wounding or death, and failure of the male gonadal development. The encounter allows one to make comparisons of the form and frequency of different postures from species to species. It also permits an assessment of the relative amount of agonistic behavior displayed by a given species. The pairing tests allow one to assess the effect of the male on the female throughout pregnancy and parturition. Again one can measure the relative social tolerance. Studies of groups allow one to observe the social tolerance throughout subsequent generations.

As discussed under Methods, most of the behavioral units described in this section involve an interchange of tactile or visual stimuli. Thus, in this investigation, consideration of presumptive auditory and chemical communication patterns has been minimized. It is understood that marking, naso-anal contact, naso-nasal contact, and, to an extent, grooming involve some chemical communication. Although auditory communication was investigated whenever the sounds were below 15 kc, ultrasonic sounds definitely were excluded in this study. Because of the incomplete nature of the sound recordings, a consideration of auditory communication will be deferred in this study.

Aspects of visual communication are difficult to evaluate among nocturnal rodents; however, the striking convergence in color patterns (especially of the tail) between the dipodid genera and the heteromyid genus *Dipodomys* deserves special comment. The kangaroo rats and jerboas have relatively large eyes, and in both groups ritualized upright postures are employed in fighting and during initial contact and courtship (see p. 23 and Eisenberg, 1963b). The white tip on the otherwise black terminal tuft of the tail appears to serve as an orientation point for a male when driving a female or when chasing another male. The white ventrum, displayed during a series of upright postures, produces a sharply contrasting reflecting surface that surely aids in orientation during sequences of mutual uprights and sparring. This latter characteristic is, however, common to all of

the species included in this study and is not unique for the kangaroo rats and jerboas.

THE ENCOUNTER.—Encounters were run between males, females, and between males and females. In general, male to male encounters result in avoidance or in fighting, with the subsequent establishment of a dominant-subordinate relationship. Female to female encounters are less predictable and the most informative encounter type is that between a male and a female (Eisenberg, 1962a, 1963b). For the purpose of this paper, I will restrict the data to the male-female encounters under two spatial conditions and two physiological conditions.

The spatial conditions include (1) an encounter in a neutral arena and (2) an encounter in a territorial box (see p. 8). Since the dimensions of the encounter arena influence the outcome (Eisenberg, 1963b), the dimensions will be specified in all tabulations.

The two physiological conditions include (1) the estrous and (2) the anestrous states of the female. In all discussions of male-female encounters the male was judged to be in a sexually viable condition.

For tabulation purposes the behavior patterns are often classified into the following categories: contact promoting, sexual, and agonistic. The composition of each category corresponds to the classification presented on page 10.

Solitary Versus Tolerant Species: If we compare a series of encounters between males and anestrous females for different species, we find evidence for a distinct separation into two social types. One type either avoids contact or, if the arena space is small, engages in agonistic behavior. The second type initiates contact-promoting behaviors such as grooming. Table 10 lists the totals and average frequencies of bouts of the major behaviors displayed during encounters in a neutral arena or a territorial box. A tolerant species such as *Peromyscus maniculatus gambelii* engages in a grooming bout approximately once per encounter even in a territorial encounter, whereas a solitary species in a neutral encounter avoids contact aside from the naso-nasal. Tables 11 and 12 demonstrate a similar separation into contact-prone and avoidance-prone social types, although here the data are selected from a carefully controlled series that utilizes the neutral arena and the territorial box experiments. In the latter situation, contact-promoting behavior drops even further and agonistic aspects become more apparent.

An inspection of tables 11 and 12 suggests that *Meriones unguiculatus*, *Gerbillus gerbillus*, and *Allactaga elator* are more contact-prone, whereas *Dipodomys panamintinus*, *Perognathus californicus*, and *Gerbillus nanus* are more avoidance-prone when the female is in an anestrous condition.

The onset of agonistic behavior is not always immediate. In figure 3, the time course of an encounter between a male and female *Perognathus parvus* is treated in consecutive 100-second intervals. One may notice that on the day preceding estrus the male exhibits contact-promoting and sexual patterns during the first 100-second and third 100-second periods. During the second and fourth 100-second

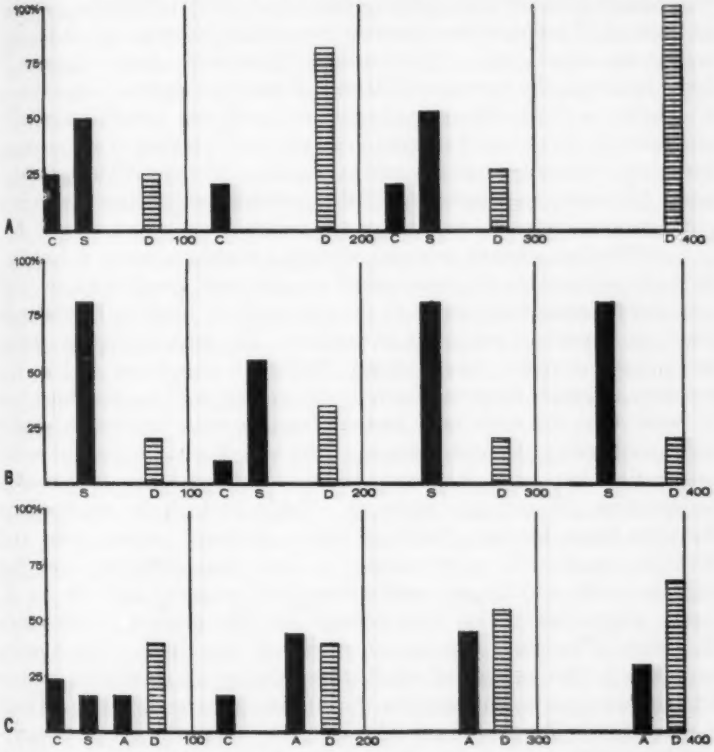


FIGURE 3.—Changing proportions of male *Perognathus parvus* behavior through the estrus cycle of his partner (A=day before estrus; B=day of estrus; C=day following estrus; ordinate=percentage of all acts for each 100-second interval; abscissa=1st, 2nd, 3rd, and 4th consecutive 100-second periods of encounter; s=all sexual acts; c=all contact-promoting acts; A=all agonistic acts; D=all individual behaviors).

periods, the male exhibits mostly individual behavior patterns that include digging and kick back, sandbathing, exploration, and sitting. On the day of estrus, sexual behaviors predominate throughout the 400 consecutive seconds. The day following estrus shows a gradual tendency for agonistic behavior to increase throughout the encounter. During the first 100 seconds, the male attempts contact and sexual

behavior; some agonistic interaction also occurs. In the second period of 100 seconds, agonistic behavior increases and some contact-promoting behavior remains. In the third and fourth 100-second periods, the male alternates between agonistic behavior and individual acts of digging and sandbathing.

The reversion to agonistic patterns on the day following estrus was examined in detail by the successive encounter technique. Tables 13 through 15 indicate the reversion to agonistic behavior or avoidance on the day after estrus. The conclusion is evident: certain species of rodents such as the heteromyid *Liomys pictus*, *Perognathus californicus*, *P. parvus*, and *Dipodomys panamintinus* and the gerbillid *Gerbillus nanus* are prone to avoid or react in an agonistic fashion to one another except for the male-estrous female situations, whereas *Allactaga elator* and *Meriones unguiculatus* exhibit contact-promoting behaviors outside of the estrous condition of the female.

Whether solitary or social, chemical communication is implied in such postures as the naso-nasal or naso-anal configurations. In such semitolerant forms as *Meriones unguiculatus*, marking by the male plays an important role in an encounter. The desert-adapted species are prone to exhibit sandbathing during an encounter and in the intolerant species there is generally an exchange of sandbathing loci in order that the male may become familiar with the female's odor before achieving physical contact. The role of sandbathing in social integration has been discussed for the Heteromyidae in previous publications (Eisenberg, 1963b, c). Table 16 includes sandbathing data for three species: *Allactaga elator*, *Meriones unguiculatus*, and *Gerbillus nanus*. It is interesting to note that significant overlap between male and female sandbathing loci occurred only in the *G. nanus* encounters. This is in accord with the general theory since *G. nanus* is the only noncontact species of the three. The species conforms to the pattern of sandbathing during an encounter as outlined in previous publications for the intolerant Heteromyidae. There can be little doubt that chemical substances left in the course of sandbathing by *G. nanus* induce further sandbathing by an approaching conspecific. The exchange of chemical signals is thus a distinct possibility.

A further consideration of tables 12 through 14 points out some interesting aspects of behavior. During a male-female encounter on the days preceding or following estrus, the male exhibits more sandbathing and/or digging and kicking back than on the day of estrus. This is especially noticeable in the encounters with *P. parvus* and *D. panamintinus*. The digging and kick-back patterns exhibit all the characteristics of classical displacement activity and often follow a bout of preliminary sexual behavior or chasing. In both of the pre-

ceding examples the primary aggressive or sexual drives are not consummated, and the male switches suddenly to an apparently meaningless pattern of digging and kicking back, often while orientated toward the female.

Species-specific Patterns of Mating Behavior: In a previous publication (Eisenberg, 1963b), a series of heteromyid rodents was compared in order to demonstrate the differences between species and genera when the frequencies of the various mating behaviors were compared. It was found that the same basic components were present in almost all forms studied, but the relative frequencies were quite different. Table 17 presents a comparison of mating patterns for eight rodent species. All data were taken from behavioral records that had terminated in a successful series of mounts. Again the conclusion is unavoidable that, although the potential exists for expression of the same motor units by almost all species, the relative frequency of occurrence of any given unit exhibits unique characteristics for the species in question. Little information can be gained on taxonomic relationships from such an analysis since, in all probability, the quantified movements are not critical releasers as is the case with many birds and fishes. The role of chemical releasers that must act in part to promote sexual isolation in small rodents (Godfrey, 1958) remains to be investigated more thoroughly.

Although complete mating in the dipodids under study was not observed, certain characteristics of their precopulatory ritual render it unique. Males of *Allactaga elator* and *Jaculus orientalis* exhibit the following courtship patterns: As the female sits stationary, the male approaches and touches his nose to hers. The male may then groom the female on the head. If the female remains stationary, the male will hop to the rear and sniff the base of her tail or, if her rump is raised, he will perform an anal-genital sniff. If the female continues to remain stationary, he will straddle her tail and mount; however, she may initiate washing or sandbathing behavior or move away. In the former case, the male will pause and then hop around her to begin again with naso-nasal contact. On the other hand, if she moves away, he will follow and commence driving. While driving, the male *Allactaga* emits a buzzing sound followed by an audible squeak, whereas the male *Jaculus* emits only the buzz. This buzzing sound is unique among all the species studied. The mating behavior of *J. jaculus* has been described in part by Lewis (1965). It appears that the male *J. jaculus* utters a "chirping" call when driving the female. During the mount, which lasts less than a minute, the male employs a neck grip with his incisors. In the example cited, Lewis reports that the couple fall to one side during the terminal phases of the mount. (Compare with *Dipodomys* in Eisenberg, 1963b.)

Copulation involves the same basic movements for all species observed; however, the temporal patterning is variable when unrelated species are compared but uniform for a given species and frequently uniform for a genus. Figures 4, 5, and 6 summarize the copulatory patterns for species of *Meriones*, *Gerbillus*, *Perognathus*, and *Dipodomys*. *Dipodomys* is characterized by a long mount, whereas the other

FIGURE 4.—Mount durations and temporal patterning of mounts for two species of *Dipodomys* (vertical bars=mount and its duration; note the protracted mount with terminal ejaculation in this species; A and B=*D. panamintinus;* C=*D. nitratoides*).

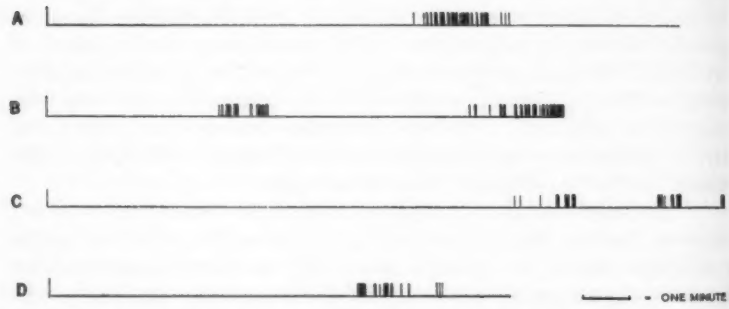


FIGURE 5.—Mount durations and temporal patterning of mounts for two species of *Perognathus* (A and B=*P. californicus;* C and D=*P. parvus*).

FIGURE 6.—Mount durations and temporal patterning of mounts for *Gerbillus* and *Meriones* (A and B=*M. unguiculatus;* C=*G. nanus*).

genera exhibit extremely short mounts. The *Perognathus* species and *Gerbillus nanus* generally have one bout of mounting with ejaculation on the terminal mount, whereas the more social *Meriones* exhibits a prolonged mount series with several apparent ejaculations. In this patterning, *Meriones* resembles the golden hamster, *Mesocricetus auratus* (Beach and Rabedaeu, 1959), and the Norway rat, *Rattus norvegicus* (Beach and Jordan, 1956).

At the time of ejaculation, the genus *Perognathus* exhibits a singular pattern. The male *P. californicus* rolls to one side while, in the case of *P. inornatus* and *P. parvus*, the female generally twists over on her side, frequently throwing the male over also.

This brief review should indicate that considerable uniformity in sexual behavior exists when species of the same genus are compared (e.g., *Perognathus* and *Dipodomys*). Table 18 summarizes the unique features of several rodent copulation patterns. Reference to this table further indicates that considerable variability can exist among the genera of a single family. At this time the adaptive significance of such differences is not apparent although one can surmise that *Dipodomys*, which exhibits such a sustained mount, surely must copulate underground in burrows.

PAIR TOLERANCE.—The data for this section were obtained by allowing a male to remain with a female throughout the parturition and rearing of the litter. Mere tolerance without fighting by a pair in the absence of reproduction was not accepted as evidence for social tolerance (see p. 3). Since the tolerance is in part a function of space, the dimensions of the cage are listed for all experiments. Further, the species ranged in size from 12 grams to 150 grams adult weight. To correct for this size bias, I have listed for each cage size two correction factors that express the area in terms of square inches per gram of animal and square inches per animal.

In general, even females of the most tolerant species will withdraw and nest separately at the time of parturition; however, tolerant species show a compatibility that permits sustained contact without extreme aggression throughout the first few hours after parturition and on through the rearing phase. Table 19 summarizes the pairing tendencies for several species prior to and through the female's estrous period. Those that exhibited solitary nesting tendencies were not paired beyond the mating; the more tolerant species were left together through parturition. This second class of data is summarized in table 20. Table 21 summarizes the data for those species that did not breed for various known and unknown reasons. The conclusions are as follows:

Regardless of the animal's size, given at least 70 to 90 square inches per animal, the normally tolerant species will conceive and remain compatible throughout parturition. The more intolerant species require greater space in order to avoid contact. One can breed the less tolerant species either by providing them with a larger space or by utilizing a series of staged encounters through a female's estrous period followed by total separation through the parturition and rearing phases (Eisenberg and Isaac, 1963).

GROUP FORMATION THROUGH INTERNAL RECRUITMENT.—By allowing a pair to reproduce in a large cage, one can further evaluate social tolerance. In general, reproduction will continue until social contacts reach such a peak that the female fails to cycle or deserts her litter. If one adult male can keep other adults away and reduce the level of contacts to which the sexually reproducing females are subjected, then reproduction will continue. This is true for communal as well as solitary species, but the latter rely on overt aggression more often than do the former and also the solitary species are much more sensitive to social interference than is the case with the more social, communal forms. Thus, a communal species in a confined space generally will exhibit an area in the cage where several sexually active females are nesting and rearing litters. A single sexually active male will have access to these females while the remainder of the population, adults and juveniles of both sexes, dwell communally and fail to reproduce. (See also descriptions for *Mus musculus*, Crowcroft and Rowe, 1963; and *Rattus norvegicus*, Calhoun, 1963a.) Eventually reproduction may cease altogether. Figures 7 and 8 demonstrate the

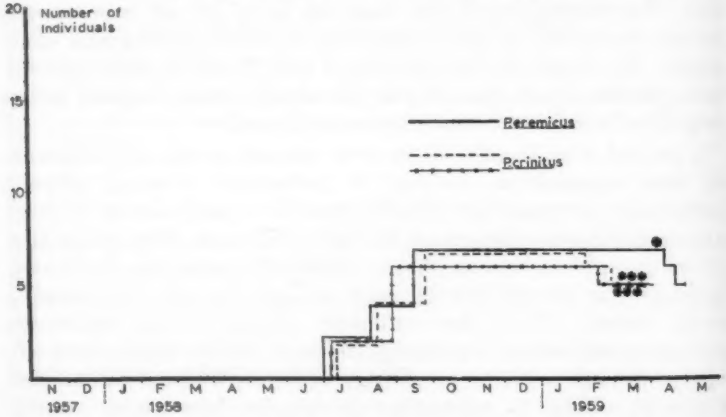


FIGURE 7.—Population growth for two species of *Peromyscus* (stars=number of individuals showing wounds during the spring fighting).

population growth of several species of *Peromyscus*. Note in several cases the tendency to form a stable plateau with a failure of reproduction. Note also, in the case of *P. crinitus*, the wounding caused by male aggression. Although not illustrated in these particular graphs, there is in some cases a slight trend to begin sexual activity at the onset of spring after a fall and winter plateau; however, as shown here the plateau holds. Table 22 includes the results of all population growth experiments with eight rodent species. Note that the rela-

tively intolerant, solitary *Dipodomys nitratoides* ceased effective reproduction with the greatest number of square inches per animal and at approximately the same grams per unit area as did the less tolerant, semisolitary *Peromyscus crinitus*.

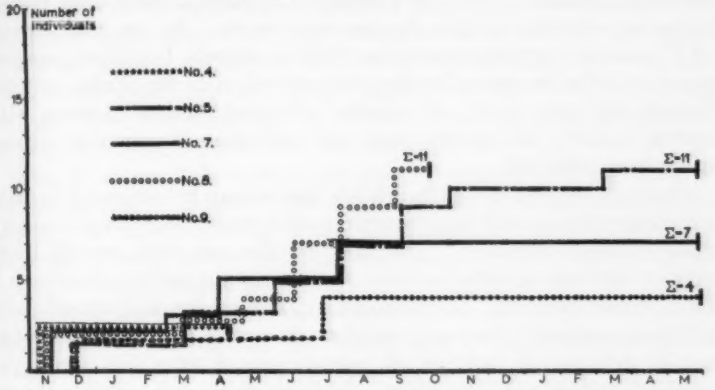


FIGURE 8.—Population growth for *Peromyscus californicus;* note the extreme stability.

An examination of the causes of population curtailment under confined conditions suggests four mechanisms: (1) During a plateau period, the females are generally anestrous with no evidence of normal estrous cycles; (2) the males born into the system show retarded gonadal maturation or even slowed growth; (3) males and even females may exhibit wounds as evidence of abnormal fighting, and such individuals may even die; (4) newborn litters may be neglected or destroyed. It would appear that different species have different thresholds of sensitivity for each of the four suggested pathologies. Thus, a solitary species, when forced to live as a pair in a small cage, may not exhibit reproduction because of a failure on the part of the female to cycle and, although they live compatibly, they are not exhibiting a natural tolerance. In a similar manner, the recruitment failure may be a result of male gonadal failure; agonistic behavior may be so intense that overt fighting and death result; and, if young are born, they may die from maternal neglect or cannibalism.

Lidicker (1965) has published the results of similar population studies utilizing *Peromyscus maniculatus*, *P. truei*, *Mus musculus*, and *Oryzomys palustris*. He concludes that species which normally do not experience high densities (or are dispersed in their native habitat) are more prone to exhibit overt fighting and cannibalism of young at high densities. My data concur in suggesting that tolerant species can form high densities with a minimum of agonistic behavior, but I believe the evidence shows that all systems of density regulation are

latent in all species and only threshold differences correlate with a given social type (see p. 29).

In both Lidicker's study (1965) and my own, the species of *Peromyscus* show a tendency to increase their reproductive activity in the spring or autumn, following a cessation of reproduction after having achieved a density limit in the previous season. In one case a group of *P. eremicus* partially reared two litters, whereas two other *eremicus* groups showed increased male-male aggression in the spring but the females did not cycle. *P. crinitus* exhibited similar patterns with spring reproduction in one case and male-male antagonism in two cases (see table 22).

One may ask if a normally solitary species can be subjected to early experience that would be conducive to the production of more socially tolerant adult behavior. This may be the case with certain labile species that are adapted to exist at varying population densities. I have found, however, that strongly solitary species will not adapt to enforced proximity even as juveniles. It is true that juvenile groups can be maintained together for long periods of time, but normal reproduction does not take place. In figure 9 one can observe the reversion to agonistic behavior within eight days after a group of

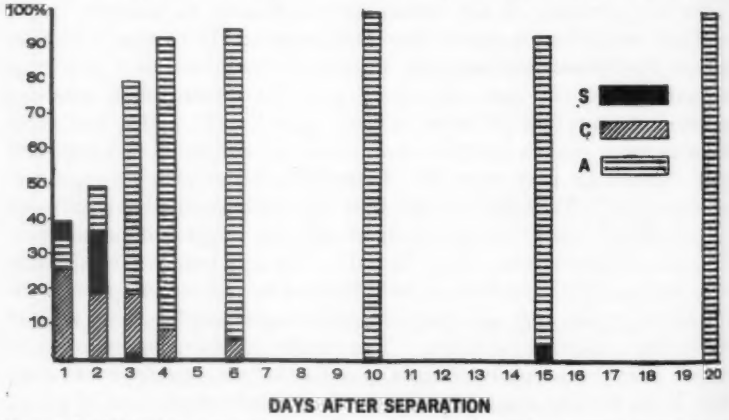


FIGURE 9.—Changing proportions of responses during *Perognathus parvus* littermate encounters after separation at 70 days of age (S=sexual behaviors; C=contact-promoting behaviors; A=agonistic behaviors).

*Perognathus parvus* littermates were separated. Not only is normal reproduction affected, but prolonged social experience often appears to have little permanent conditioning effect with this species and others. Littermate groups of typically solitary rodents that did not exhibit normal reproduction included *Perognathus parvus*, *Dipodomys nitratoides*, *Gerbillus nanus*, and *Liomys pictus*.

DISCUSSION.—As stated in the introduction to this section, rodent social systems may be classified as solitary, pair tolerance, and communal. The latter two represent in extreme form a closed social grouping, impermeable to outsiders. In reality there are rodent species that, as species, exhibit so-called loose social systems wherein the species may oscillate between a more dispersed solitary formation or a more tolerant, semicommunal system—depending upon the environmental conditions and the population density. The data from the current studies permit me to attempt several generalizations cast against the background of this social classification.

First, it appears that what separates a socially tolerant from a solitary species is the ability of the former to overcome an initially agonistic or avoidance interaction by means of special behavioral mechanisms to insure contact and familiarity without the danger of fighting. Among these mechanisms grooming appears to be important. Furthermore, a social species can achieve contact in the absence of primary sexual stimuli. A solitary species is either unable to achieve contact or, if it does, it is stressed to some extent; and, under conditions of prolonged contact, the physiological mechanisms governing the reproductive capacity break down. This difference between the extreme forms of solitary and social species is not viewed as absolute but rather as a result of differences in sensitivity to contact. Table 23 summarizes this concept whereby the same physiological pathologies are considered for each major social type.

A second generalization concerns the probable outcome of the various social tests if applied to a species of each major social type. Table 24 summarizes these predictions, which are drawn from the data in the previous section. In table 25 the species included in this study are ranked as to social tolerance according to the field and laboratory data.

## General Discussion

The behavioral survey of the present study group has shown considerable uniformity in the orientation movements and fixed action patterns. Definite differences in fixed action patterns are usually correlated with corresponding differences in morphology as, for example, in bipedal locomotion. Even in such a markedly specialized behavior pattern, normally quadrupedal species have the capacity to assume a bipedal stance and even hop for a short distance. When we consider sandbathing as a fixed action pattern, we find that it is composed of two to three distinct movements that are part of the behavioral inventory of almost all mammals, and only a unique combination of these components results in a species- or taxon-specific behavior.

When we turn to social interactions, again it appears that the presence or absence of certain movements as an arbitrary criterion will not always suffice to delineate species or serve as a taxonomic tool. This results, no doubt, from the fact that small nocturnal rodents rely less on visual display in communication and, hence, less on visual releasers in sexual isolation with the result that spectacular differences in the fixed action patterns, observable in some avian and fish taxa, are not to be found. Certainly visual communication by movements, postures, and coat color are important in some mammalian taxa such as the primates and ungulates, but they are obviously less important in the small, nocturnal mammalian taxa. Again and again in this study, species-specific behavior patterns are found to be variations on universal neuromuscular patterns. Differences and similarities in the frequency of expression are more reliable indicators of nonrelationship or affinity than is the criterion of presence or absence of expression. In some cases even a frequency analysis fails to indicate affinity above the generic level, for example, in the temporal patterning of copulation. Thus, employing the presence or absence criterion, some behavior patterns will be family-specific, others genus-specific, and even more rarely a pattern will be species-specific; however, analysis of the discrete temporal patterning or relative frequency of occurrence almost always will demonstrate species differences although the adaptive significance of such differences may be unclear (consider again sandbathing). Since such an equipotentiality exists in the repertoires of these mammals—although frequency of occurrence serves to clearly delineate species—I can only conclude that differences in thresholds exist that account for the differential frequencies of expression. Thus, the behavior of a given species may be described in terms of the most probable sequence or set of patterns rather than in terms of its total potentiality for expression. In this sense, species-specific behavior describes the normal expression for a given environment and conforms to Leyhausen's "Verhaltenshäufigkeit" (Leyhausen, 1965).

By applying this definition of species-specific behavior to the social structure observed in different species, it is possible to characterize a given species as belonging to one of several categories of social behavior. For example, *Perognathus parvus* can be kept in groups with little overt fighting. This is especially true if the group is composed of littermates. Although they can tolerate one another, they do not reproduce. Utilizing reproductive success as the criterion for a natural social grouping, we can conclude that, although *P. parvus* has a range tolerance that permits group life without overt aggression leading to wounding, it does not have the ability to reproduce when subjected to social contacts above some minimum level. In the case of this species, the minimum appears to be only the pair association

through estrus. Thus, as outlined in the previous section, there are probably several physiological mechanisms that are affected adversely in terms of reproductive success by social contacts. The relative thresholds for these mechanisms varies from species to species depending on their genetic makeup.

The adverse effects of high population densities on the growth and maturation of young rodents has been known for some time (Chitty, 1955), and the cessation of reproduction at high densities through a failure of ovarian and testicular function has been studied from a physiological standpoint by many workers (see Christian, 1963). Recently Calhoun (1963b) has developed an elaborate theory of social behavior based on the concepts of species-specific differences in social tolerance and the evolution of social groups. Wynne-Edwards (1962) has put forth an all-embracing theory on evolution of social groups and the adaptive value of self-regulatory mechanisms whereby populations are kept below maximum numbers by such reproductive failures as outlined previously. I do not wish to examine these various theories from a critical standpoint but only wish to point out that the evidence favors my interpretation of species differences in social tolerance and, further, that these differences have resulted from processes of natural selection to produce a social type adapted to its particular niche. I have attempted to outline a methodology whereby one can study social tolerance by means of several techniques and arrive at some quantitatively based conclusions regarding species differences in sociability.

There remains a further consideration. Given the demonstration that the rodents under study exhibit species-specific social tendencies, what adaptive correlates can one discern? The arid-adapted subfamily Gerbillinae spans the range from a relatively solitary form, *Gerbillus nanus*, to the more tolerant, communal *Tatera indica*. *Jaculus orientalis* and *Allactaga elator* are semitolerant; however, the family Heteromyidae, whether forest-adapted or arid-adapted, appears to be a solitary form. Within the genus *Peromyscus*, the desert species *P. crinitus* is intolerant whereas the equally xeric-adapted *P. eremicus* is more tolerant. Adaptation to xeric habitats with dispersed food supplies is not necessarily in and of itself conducive to selection for a dispersed, solitary existence. Equally important are other aspects of the species ecology including its mode of assembly of foodstuffs, its shelter construction, and its reproductive rate. At this point it seems safe to say that the Heteromyidae have retained the phylogenetically ancient trait of solitary existence because of the adaptive advantage accruing from its defense of cached food. It is not the case, however, that this social trait is always a concomitant of caching.

It is noteworthy that *Gerbillus* (*Dipodillus*) *nanus* resembles the silky pocket mice of the heteromyid genus *Perognathus* in several

respects. *G. nanus* is sensitive to crowding, and captive reproduction is possible only by means of a simultaneous encounter technique. During male-anestrous female encounters, the partners exhibit mutual avoidance or agonistic patterns of behavior. Sandbathing as a means of chemical communication is displayed by this species and, after mating, the male and female return to behavior patterns expressing intolerance. All the preceding attributes also characterize the behavior of *Perognathus parvus*, *P. inornatus*, and *P. longimembris* (see p. 22 and Eisenberg, 1963b). Returning again to tables 2 through 5, there is a marked similarity between *G. nanus* and the silky pocket mice with respect to habitat, general ecology, size, and reproduction. This total convergence may well be indicative of a special adaptation syndrome that correlates with the attribute of social intolerance; however, until further comparisons are made on the energy needs and recruitment rates of different desert-adapted species, the selective advantage of the various social systems in all probability will remain obscured.

## Summary

Selected species from three rodent families have been studied, including the following genera: Cricetinae: *Peromyscus;* Gerbillinae: *Tatera*, *Gerbillus*, *Dipodillus*, *Pachyuromys*, and *Meriones;* Dipodidae: *Jaculus*, *Allactaga;* Heteromyidae: *Heteromys*, *Liomys*, *Perognathus*, and *Dipodomys*. Species have been selected in order to give a series of forms that have evolved in a convergent or parallel fashion in adapting to desert environments.

The discrete behavior patterns exhibit a profound similarity, but species and generic differences can be discerned. Sandbathing has been selected for intensive study and it has been found that functional sandbathing has evolved independently in all xeritic-adapted forms from the same basic movement patterns. Differences in the frequency of occurrence rather than in the form of the movement have proved to be the most effective criterion for delineating taxon-specific differences.

Social behavior has been investigated with a standard methodology including staged encounters, pair tolerance, and group formation tests. Using reproductive success as the criterion for describing a functional social group, it has been found that each species can be characterized into one of three general social types. The different social types appear to represent different degrees of tolerance for the presence of conspecifics. All social types will exhibit similar social pathologies under social stress, but the more social species have higher thresholds of tolerance. It is proposed that species-specific social tolerance represents an adaptation to average densities that are of selective advantage to the species under consideration. The adaptive correlates of the differing social systems remain, in part, unknown.

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TABLE 1.—*List of species in the present study with geographical origins and comments on maintenance*

| Species | Original numbers | | Origin | Number of captive bred litters | Comments on maintenance |
|---|---|---|---|---|---|
| | Males | Females | | | |
| CRICETINAE | | | | | |
| *Peromyscus maniculatus* | 6 | 7 | Alameda Co., Calif. | 30+ | see Eisenberg (1962a, 1963a) |
| *californicus* | 5 | 6 | Alameda Co., Calif. | 22+ | " |
| *eremicus* | 2 | 4 | San Diego Co., Calif. | 9 | " |
| *crinitus* | 2 | 3 | San Bernardino Co., Calif. | 8 | " |
| HETEROMYIDAE | | | | | |
| *Heteromys lepturus* | 0 | 2 | Cintapec in Veracruz, Mexico | – | see Eisenberg (1963b) |
| *anomalus* | 2 | 2 | Trinidad, B.W.I. | 0 | " |
| *desmarestianus* | 2 | 1 | Costa Rica | 0 | as *anomalus* |
| *Liomys pictus* | 3 | 6 | Mazatlan in Sinaloa, Mexico | 7 | see Eisenberg (1963b) |
| *Perognathus californicus* | 4 | 2 | Santa Cruz and San Benito Cos., Calif. | 3 | " |
| *inornatus* | 1 | 2 | San Benito and San Joaquin Cos., Calif. | 0 | " |
| *parvus* | 8 | 4 | Oliver, B.C., Canada | 2 | as *inornatus* |
| *Microdiopodops pallidus* | 7 | 4 | Mineral and Churchill Cos., Nev. | 0 | see Eisenberg (1963b) |
| *Dipodomys merriami* | 3 | 4 | San Diego and Kern Cos., Calif. | 3 | " |
| *nitratoides* | 4 | 3 | San Benito and Kern Cos., Calif. | 12 | " |
| *panamintinus* | 3 | 2 | Kern Co., Calif. | 2 | " |
| GERBILLINAE | | | | | |
| *Gerbillus gerbillus* | 2 | 1 | Abu Rawash, Egypt | 0 | as *Perognathus* |
| (*Dipodillus*) *nanus* | 5 | 7 | West Pakistan | 1 | " |
| *Meriones unguiculatus* | 10 | 10 | laboratory stock | 5 | as *Peromyscus* |
| *hurrianae* | 2 | 2 | West Pakistan | 7 | " |
| *Pachyuromys duprasi* | 1 | 0 | North Africa | – | as *Perognathus* |
| *Tatera indica* | 3 | 2 | West Pakistan | 11 | as *Peromyscus* |
| DIPODIDAE | | | | | |
| *Allactaga elator* | 5 | 2 | West Pakistan | 0 | as *Dipodomys* |
| *Jaculus jaculus* | 2 | 0 | Abu Rawash, Egypt | – | " |
| *orientalis* | 1 | 1 | Amariya, Egypt | 1 | " |

TABLE 2.—*Comparisons of reproduction*

| Species | Gestation (days) | Age at eye opening (days) | Litter size | Authority |
|---|---|---|---|---|
| CRICETINAE | | | | |
| *Peromyscus maniculatus* | 22–24 | 11–16 | 2–9 | present study |
| *crinitus* | 24 | 12–15 | 3–5 | " " |
| *eremicus* | 21 | 12–14 | 2–4 | " " |
| *californicus* | 21–25 | 14–16 | 1–3 | " " |
| GERBILLINAE | | | | |
| *Gerbillus nanus* | 23 | 14–15 | 3 | " " |
| *Tatera indica* | 26 | 17–19 | 3–8 | " " |
| *Meriones unguiculatus* | 25 | 17–19 | 3–6 | " " |
| *hurrianae* | 25 | 14–15 | 5–7 | " " |
| *Pachyuromys duprassi* | 21 | 20–21 | – | Petter (1961) |
| HETEROMYIDAE | | | | |
| *Heteromys melanoleucus* | ? | 20–21 | ca. 4 | Rood (1963) |
| *desmarestianus* | ? | ? | 3–4 | Eisenberg (1963b) |
| *Liomys pictus* | 24–26 | 18–21 | 2–5 | " |
| *Perognathus californicus* | 25 | 14–16 | 2–5 | " |
| *parvus* | 24–25 | 14–15 | 2–8 | present study |
| *Dipodomys merriami* | 33 | 11–12 | av. 2 | Eisenberg (1963b) |
| *nitratoides* | 32 | 10–11 | av. 2 | " |
| *panamintinus* | 29 | 17–18 | 3–4 | " |
| DIPODIDAE | | | | |
| *Allactaga elator* | ? | – | 2–6 | Ognev (1963) |
| *Jaculus orientalis* | 28–30 | 35–36 | 3–7 | present study and Kirmiz (1962) |

TABLE 3.—*Comparisons of morphology*

| Species | Adult weights (gms) [1] | Ratio of hind foot length to body length [2] |
|---|---|---|
| CRICETINAE | | |
| *Peromyscus maniculatus* | 18–34 | .23 |
| *crinitus* | 14–23 | .25 |
| *eremicus* | 18–24 | .24 |
| *californicus* | 35–40 | .24 |
| GERBILLINAE | | |
| *Gerbillus gerbillus* | 25–49 | .35 |
| *nanus* | 15–36 | .30 |
| *Tetera indica* | 70–150 | .23 [3] |
| *Meriones unguiculatus* | 76–95 | .25 [3] |
| *hurrianae* | 60–95 | .25 [3] |
| *Pachyuromys duprassi* | 30–65 | – |
| HETEROMYIDAE | | |
| *Heteromys anomalus* | 45–60 | – |
| *desmarestianus* | 61–78 | .26–.28 |
| *Liomys pictus* | 35–51 | .21–.24 |
| *Perognathus californicus* | 18–25 | .31 |
| *parvus* | 17–26 | .27 |
| *inornatus* | 10–18 | .27 |
| *Microdipodops pallidus* | 10–16 | .37 |
| *Dipodomys nitratoides* | 28–43 | .36 |
| *merriami* | 30–40 | .36 |
| *panamintinus* | 44–68 | .32–.33 |
| DIPODIDAE | | |
| *Allactaga elator* | 45–71 | $\geq$.50 [3] |
| *Jaculus jaculus* | 50–80 | $\geq$.50 [3] |
| *orientalis* | 130–225 | $\geq$.50 [3] |

[1] Based on captive weights, which average higher than field weights.
[2] Computed from measurements in Petter (1961), Eisenberg (1963b), Hall and Kelson (1959).
[3] Taken from Hatt (1932).

TABLE 4.—*Comparisons of habitat*

| Species | Habitat type | Authority |
|---|---|---|
| CRICETINAE | | |
| *Peromyscus maniculatus gambelii* | Oak-woodland, chaparral | Eisenberg, 1962a |
| *crinitus stephensi* | High altitude desert | Eisenberg, 1963a |
| *eremicus eremicus* | Low altitude desert | " " |
| *californicus parasiticus* | Oak-woodland, chaparral | Eisenberg, 1962a |
| GERBILLINAE | | |
| *Gerbillus gerbillus* | Sand desert | Zahavi and Wahrman, 1957 |
| *nanus* | Soil desert | " |
| *Tatera indica* | Semidesert, near water sources | Petter, 1961 |
| *Meriones unguiculatus* | Semidesert | Deduced from range maps |
| *hurrianae* | Semidesert | Petter, 1961 |
| *Pachyuromys duprassi* | Sand and soil desert | " " |
| HETEROMYIDAE | | |
| *Heteromys* (all species) | Tropical evergreen forest | Eisenberg, 1963b |
| *Liomys pictus* | Subtropical thorn forest | " " |
| *Perognathus californicus* | Semiarid to arid brush | " " |
| *inornatus* | Seasonally arid grassland | " " |
| *parvus* | Semidesert | " " |
| *Microdipodops pallidus* | High altitude, sand desert | " " |
| *Dipodomys merriami* | Seasonally arid grassland to sand desert | " " |
| *nitratoides* | Seasonally arid grassland to sand desert | " " |
| *panamintinus* | High altitude pebble desert | " " |
| DIPODIDAE | | |
| *Allactaga elator* | Pebble desert | Ognev, 1963 |
| *Jaculus jaculus* | Desert | Kirmiz, 1962 |
| *orientalis* | Desert | " " |

TABLE 5.—*General comparisons of behavior and ecology*

| Species | Activity period | Food preference | Water source | Hibernation |
|---|---|---|---|---|
| CRICETINAE | | | | |
| *Peromyscus* (all species) | Nocturnal | Seeds | Needs free water or succulents | No [1] |
| GERBILLINAE | | | | |
| *Gerbillus gerbillus* | " | Seeds | Metabolic water | No |
| *nanus* | " | Seeds and insects | " " | No |
| *Tatera indica* | " | Seeds | Succulent plants | No |
| *Meriones urquiculatus* | Semidiurnal | Seeds and insects | " " | No |
| *hurrianae* | " | " " " | " " | No |
| *Pachyuromys duprassi* | Nocturnal | " " " | Metabolic water(?) | (?) |
| HETEROMYIDAE | | | | |
| *Heteromys* (all species) | " | Seeds and green plants | Needs free water | No |
| *Liomys pictus* | " | " | Free water or succulents | No |
| *Perognathus californicus* | " | Seeds and insects | Can live on metabolic water | Periods of torpor |
| *parvus* | " | " " " | " | Yes |
| *inornatus* | " | " " " | " | Periods of torpor |
| *Microdipodops pallidus* | " | " " " | " | Yes |
| *Dipodomys merriami* | " | Seeds | " | No |
| *nitratoides* | " | " | " | No |
| *panamintinus* | " | " | " | No |
| DIPODIDAE | | | | |
| *Allactaga elator* | " | " | Metabolic water | Yes |
| *Jaculus jaculus* | " | " | " " | Periods of torpor |
| *orientalis* | " | " | " " | " |

[1] *P. eremicus* can exhibit seasonal torpor (see Macmillan, 1965).

TABLE 6.—*Comparisons of sandbathing movements*

| Species | Number of subjects | Number of observation periods | Average time of observation period (seconds) | Total number of acts | Proportion of total | |
|---|---|---|---|---|---|---|
| | | | | | Side rubs | Ventral rubs |
| DIPODIDAE | | | | | | |
| *Allactaga elator* | 3 | 62 | 249 | 274 | .920 | .080 |
| HETEROMYIDAE | | | | | | |
| *Dipodomys deserti* | 2 | 38 | 340 | 425 | .675 | .325 |
| *nitratoides* | 2 | 11 | 456 | 261 | .61 | .39 |
| *Perognathus californicus* | 4 | 51 | 308 | 305 | .55 | .45 |
| *parvus* | 14 | 45 | 263 | 112 | .77 | .23 |
| GERBILLINAE | | | | | | |
| *Meriones unguiculatus* | 11 | 37 | 372 | 44 | 1.00 | .00 |
| *Gerbillus nanus* | 4 | 51 | 270 | 189 | .99 | .01 |

TABLE 7.—*Integration of sandbathing movements*

| Species | Number of couplets beginning with a side rub | Proportion of total | | |
|---|---|---|---|---|
| | | Side rub followed by— | | |
| | | Opposite side | Same side | Ventrum |
| DIPODIDAE | | | | |
| *Allactaga elator* | 113 | .49 | .42 | .09 |
| HETEROMYIDAE | | | | |
| *Dipodomys* | | | | |
| *deserti* | 133 | .35 | .20 | .44 |
| *nitratoides* | 96 | .21 | .60 | .19 |
| *Perognathus* | | | | |
| *californicus* | 126 | .37 | .21 | .42 |
| *parvus* | 71 | .45 | .18 | .36 |
| GERBILLINAE | | | | |
| *Meriones unguiculatus* | 13 | 1.00 | 0 | 0 |
| *Gerbillus nanus* | 55 | .88 | .12 | 0 |

TABLE 8.—*Similarities in maintenance behavior* (O=not observed, X=occasionally observed, XX=typical behavior)

| Species | Incisor and snout tamping in borrow construction | Chopping of foodstuffs | Caching | Bipedal locomotion |
|---|---|---|---|---|
| CRICETINAE | | | | |
| *Peromyscus* [1] | 0 | 0 | XX | 0 |
| GERBILLINAE | | | | |
| *Meriones unguiculatus* | X | XX | X | 0 |
| *hurrianae* | X | XX | X | 0 |
| *Tatera indica* | X | XX | X | 0 |
| *Gerbillus nanus* | 0 | 0 | X | 0 |
| *gerbillus* | 0 | 0 | XX | 0 |
| *Pachyuromys duprassi* | 0 | 0 | X | 0 |
| DIPODIDAE | | | | |
| *Jaculus jaculus* | XX | 0 | 0 | XX |
| *orientalus* | XX | 0 | 0 | XX |
| *Allactaga elator* | XX | 0 | X | XX |
| HETEROMYIDAE | | | | |
| *Heteromys* [1] | 0 | 0 | XX | 0 |
| *Liomys* [1] | 0 | 0 | XX | 0 |
| *Perognathus* [1] | 0 | 0 | XX | 0 |
| *Microdipodops pallidus* | 0 | 0 | XX | XX |
| *Dipodomys* [1] | 0 | 0 | XX | XX |

[1] All species studied.

TABLE 9.—*Similarities in marking and sandbathing* (all components are shown by all species when fur is wet, a phenomenon not considered in the present comparison; O=not noted, X=occasional, XX=typical of most sequences)

| Species | Integrated components in functional pelage dressing with a secondary marking function | | | Marking movements which are generally independent of pelage dressing | | |
|---|---|---|---|---|---|---|
| | Ventrum rub | Side rub | Rolling over | Ventrum rub | Side rub | Perineal drag |
| CRICETINAE | | | | | | |
| *Peromyscus maniculatus* | 0 | 0 | 0 | 0 | 0 | XX |
| *californicus* | 0 | 0 | 0 | 0 | 0 | XX |
| *eremicus* | 0 | 0 | 0 | 0 | 0 | XX |
| *crinitus* | 0 | XX | 0 | 0 | 0 | XX |
| GERBILLINAE | | | | | | |
| *Meriones unguiculatus* | 0 | XX | X | XX | 0 | XX |
| *hurrianae* | 0 | XX | X | XX | 0 | XX |
| *Gerbillus gerbillus* | 0 | XX | 0 | 0 | 0 | XX |
| *nanus* | 0 | XX | 0 | 0 | 0 | XX |
| *Tatera indica* | X | XX | X | 0 | 0 | XX |
| *Pachyuromys duprassi* | 0 | XX | X | 0 | 0 | XX |
| DIPODIDAE | | | | | | |
| *Allactaga elator* | X | XX | 0 | 0 | 0 | XX |
| *Jaculus jaculus* | X | XX | 0 | 0 | 0 | XX |
| *orientalis* | X | XX | 0 | 0 | 0 | XX |
| HETEROMYIDAE | | | | | | |
| *Heteromys anomalus* | 0 | 0 | 0 | X | 0 | XX |
| *lepturus* | 0 | 0 | 0 | X | 0 | XX |
| *Liomys pictus* | 0 | 0 | 0 | X | X | XX |
| *Perognathus* [1] | XX | XX | 0 | 0 | 0 | XX |
| *Microdipodops* [1] | XX | XX | 0 | 0 | 0 | XX |
| *Dipodomys* [1] | XX | XX | 0 | 0 | 0 | XX |

[1] All species studied.

TABLE 10.—*Response totals for male-anestrous female encounters in a neutral arena* (parentheses enclose the average number of bouts per encounter)

| Species | Number of encounters | Duration of encounter | Total and average frequency of behavior pattern | | | |
|---|---|---|---|---|---|---|
| | | | Grooming | Uprights | Chase | Fight |
| *Peromyscus maniculatus* [1] | 18 | 30 min. | 17(.9) | 34(1.9) | 15(.8) | 4(.2) |
| *Liomys pictus* | 21 | " | 2(.1) | 7(.3) | 85(4.0) | 7(.3) |
| *Dipodomys panamintinus* | 19 | " | 2(.1) | 15(.8) | 43(2.3) | 2(.1) |
| *Microdipodops pallidus* | 14 | " | 2(.1) | 13(.9) | 19(1.3) | 2(.1) |

[1] Territorial encounter only, which accounts for the rather high level of chasing that occurred prior to the grooming relationship.

TABLE 11.—*Response totals for males in a male-anestrous female encounter* (counts made for the first 200 seconds of the encounter only; all data from a neutral arena; parentheses enclose the average number of bouts per encounter)

| Species | Number of encounters | Range and average frequency of behavior pattern | | | | |
|---|---|---|---|---|---|---|
| | | Naso-nasal | Naso-anal | Grooming | Chase-flight | Fight |
| *Meriones unguiculatus* | 16 | 3-10(6.4) | 0-9(3.2) | 1-7(2.9) | 0-2(.3) | 0 |
| *Gerbillus gerbillus* | 2 | 6-7(6.5) | 1-5(3.0) | 1(1.0) | 0(0) | 0-2(1.0) |
| *nanus* | 20 | 1-14(4.4) | 0-2(.2) | 0-3(.5) | 0-2(.7) | 0 |
| *Dipodomys panamintinus* | 6 | 0-2(.5) | 0-10(2.5) | 0 | 0-9(2.0) | 0 |

TABLE 12.—*Response totals for males in a male-anestrous female encounter* (counts made for the first 200 seconds of the encounter only; all data from a territorial encounter box; parentheses enclose the average number of bouts per encounter)

| Species | Number of encounters | Range and average frequency of behavior pattern | | | | |
|---|---|---|---|---|---|---|
| | | Naso-nasal | Naso-anal | Grooming | Chase-flight | Fight |
| *Gerbillus nanus* | 9 | 1-3(.8) | 0 | 0-1(.1) | 0-4(1.4) | 0-4(.4) |
| *Allactaga elater* | 9 | 0-7(2.7) | 0-6(1.1) | 0-3(1.0) | 0-1(.1) | 0 |
| *Perognathus californicus* | 15 | 0-1(.07) | 0-2(.26) | 0 | 0-6(2.4) | 0-19(5.6) |
| *Meriones unguiculatus* | 3 | 1-2(1.3) | 1-2(1.3) | 1-2(1.3) | 0 | 0 |

TABLE 13.—*Behavioral changes exhibited by the male* Dipodomys panamintus *through estrus in male-female encounters* (NN=Naso-nasal, NA=Naso-anal, H/H=Head over head under, NAm=Mutual naso-anal, Cu=Crawling under, Gr=Grooming, Dr=Driving, Mnt=Mounting, Thr=Mounts with thrusting, Ch=Chase and attack leaps, Fi=Fight, Fl=Flight and escape leaps, Up=Upright, SB=Sandbathing, DK=Digging and kick back, W=Washing (exclusive of postcopulatory wash), M=Marking, Si=Sitting, Ex=Exploring)

| Date | Total number of acts | Duration of encounter (secs) | Percent of total for each pattern | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Contact promoting | | | | | | Sexual | | |
| | | | NN | NA | H/H | NAm | Cu | Gr [2] | Dr [3] | Mnt | Thr |
| VI/25/63 | 55 | 360 | 1.8 | 1.8 | 0 | 0 | 0 | - | 10.9 | 0 | 0 |
| VI/26/63 [1] | 171 | 780 | .58 | 14.6 | 11.1 | 0 | 29.8 | - | 27.5 | 0 | 0 |
| VI/27/63 | 42 | 330 | 0 | 0 | 0 | 0 | 0 | - | 2.4 | 0 | 0 |
| VII/9/63 | 50 | 330 | 0 | 0 | 4.0 | 0 | 0 | - | 12.0 | 0 | 0 |
| VII/10/63 [1] | 201 | 1260 | 0 | 4.5 | 11.9 | 0 | 6.9 | - | 16.4 | .99 | 25.4 |
| VII/10/63 [1] | 70 | 1966 | 0 | 0 | 4.3 | 0 | 0 | - | 1.4 | 20.0 | 61.4 |
| VII/11/63 | 14 | 22 | 0 | 0 | 0 | 0 | 0 | - | 0 | 0 | 0 |

| Date | Total number of acts | Duration of encounter (secs) | Percent of total for each pattern | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Agonistic | | | | Individual | | | | | |
| | | | Ch [3] | Fl | Fl [3] | Up | SB [3] | DK [3] | W [3] | M | Si [3] | Ex [3] |
| VI/25/63 | 55 | 360 | 37.8 | 0 | 4.7 | 0 | 1.82 | 14.5 | 1.82 | 3.6 | 9.1 | 10.9 |
| VI/26/63 [1] | 171 | 780 | 9.9 | 1.2 | 0 | 0 | 0 | 14.0 | 0 | 2.3 | .58 | 0 |
| VI/27/63 | 42 | 350 | 38.0 | 0 | 0 | 0 | 2.4 | 33.4 | 0 | 0 | 11.9 | 11.9 |
| VII/9/63 | 50 | 330 | 34.0 | 2.0 | 4.0 | 0 | 2.0 | 14.0 | 0 | 2.0 | 26.0 | 0 |
| VII/10/63 [1] | 201 | 1260 | 6.3 | .5 | 1.5 | 0 | 0 | 7.0 | 0 | .5 | 13.4 | 2.0 |
| VII/10/63 [1] | 70 | 1966 | 8.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2.9 | 0 |
| VII/11/63 | 14 | 22 | 50.0 | 0 | 0 | 0 | 7.2 | 21.4 | 7.2 | 7.2 | 0 | 7.2 |

[1] Date of estrus.

[2] Grooming during head over head under and mount.

[3] Ten seconds or less in duration was counted as one bout (see Methods).

TABLE 14.—*Behavioral changes exhibited by male of* Perognathus parvus *through estrus in a male-female encounter* (see table 13 for abbreviations)

| Date | Total number of acts | Duration of encounter (secs) | Percent of total for each pattern: Contact promoting NN | NA | H/H | NAm | Cu | Gr | Sexual Dr[2] | Mnt | Thr |
|---|---|---|---|---|---|---|---|---|---|---|---|
| II/3/63 | 117 | 940 | 7.7 | 0 | 0 | 0 | 0 | 1.7 | 7.7 | 2.6 | 0 |
| II/5/63[1] | 102 | 770 | 9.8 | 0 | 0 | 0 | 0 | 1.0 | 14.7 | 8.8 | 5.9 |
| II/7/63 | 53 | 400 | 9.4 | 0 | 0 | 0 | 0 | 0 | 5.7 | 0 | 0 |
| II/14/63 | 30 | 270 | 10.0 | 0 | 0 | 0 | 0 | 0 | 3.3 | 13.3 | 0 |
| II/15/63 | 23 | 210 | 0 | 0 | 0 | 0 | 0 | 0 | 13.0 | 17.3 | 0 |
| II/18/63[1] | 84 | 660 | 8.3 | 0 | 0 | 0 | 0 | 5.9 | 9.5 | 7.1 | 4.8 |
| II/21/63 | 79 | 630 | 16.5 | 0 | 0 | 0 | 0 | 5.0 | 22.8 | 10.2 | 0 |

| Date | Total number of acts | Duration of encounter (secs) | Percent of total for each pattern: Agonistic Ch[2] | Fl | Fl[2] | Up | Individual SB[2] | DK[2] | W[2] | M | Sl[2] | Ex[2] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| II/3/63 | 117 | 940 | 4.3 | 0 | 0 | 2.6 | 10.3 | 4.3 | 7.7 | .9 | 50.4 | 0 |
| II/5/63[1] | 102 | 770 | 3.9 | 0 | 0 | 6.9 | 2.9 | 1.9 | 1.9 | 1.0 | 37.3 | 0 |
| II/7/63 | 53 | 400 | 15.1 | 0 | 0 | 11.3 | 11.3 | 11.3 | 11.3 | 3.8 | 20.8 | 0 |
| II/14/63 | 30 | 270 | 0 | 3.3 | 10.0 | 0 | 0 | 0 | 0 | 0 | 56.8 | 3.3 |
| II/15/63 | 23 | 210 | 0 | 4.3 | 8.7 | 0 | 0 | 4.4 | 0 | 0 | 43.5 | 8.8 |
| II/18/63[1] | 84 | 660 | 15.5 | 0 | 0 | 2.4 | 1.2 | 2.4 | 7.1 | 0 | 34.6 | 7.1 |
| II/21/63 | 79 | 630 | 0 | 2.5 | 7.6 | 11.4 | 0 | 3.8 | 1.3 | 0 | 19.0 | 0 |

[1] Date of estrus.
[2] Ten seconds or less in duration was counted as one bout (see Methods).

TABLE 15.—*Behavioral changes exhibited by male of* Gerbillus nanus *through estrus in a male-female encounter*[2] (see table 13 for abbreviations)

| Date | Total number of acts | Duration of encounter (secs) | Percent of total for each pattern: Contact promoting NN | NA | H/H | NAm | Cu | Gr | Sexual Dr[2] | Mnt | Thr |
|---|---|---|---|---|---|---|---|---|---|---|---|
| XII/19/63 | 10 | 290 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| I/9/64[1] | 211 | 890 | 17.5 | 0 | 0 | 0 | 0 | 0 | 36.0 | 13.3 | 1.9 |
| I/11/64 | 10 | 75 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| Date | Total number of acts | Duration of encounter (secs) | Percent of total for each pattern: Agonistic Ch[2] | Fl | Fl[2] | Up | Individual SB[2] | DK[2] | W[2] | M |
|---|---|---|---|---|---|---|---|---|---|---|
| XII/19/63 | 10 | 290 | 20.0 | 0 | 60 | 0 | 20.0 | 0 | 0 | 0 |
| I/9/64[1] | 211 | 890 | .47 | 1.0 | .47 | 3.3 | .47 | 2.4 | 11.4 | .47 |
| I/11/64 | 10 | 75 | 0 | 100 | 0 | 0 | 0 | 0 | 0 | 0 |

[1] Date of estrus.
[2] Ten seconds or less in duration was counted as one bout (see Methods).

TABLE 16.—*Tendency to sandbathe at same locus during a male-female encounter*[1]

| Species | Number of encounters with sandbathing | Average number of male loci | Average number of female loci | Percent of overlap |
|---|---|---|---|---|
| *Gerbillus nanus* | 10 | 1.3 | 1.2 | 50 |
| *Allactaga elator*[2] | 3 | 1.0 | – | – |
| *Meriones unguiculatus*[2] | 9 | 1.0 | 1.25 | 0 |

[1] For similar data from the Heteromyidae, see Eisenberg, 1963c.
[2] These species have been known to exchange sandbathing loci, but this tendency is of infrequent occurrence.
[3] Side rubbing only.

TABLE 17.—*Comparisons of male contact-promoting and sexual behaviors for selected species of rodents* (Data from male-female encounters when female in pro-estrus or estrus; see table 12 for abbreviations)

| Species | Number of encounters | Total acts recorded | Relative proportion of each behavior pattern for all bouts of contact-promoting and sexual behavior recorded | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | NN | NA | H/H | NAm | Cu | Gr[1] | Dr | Mnt |
| *Liomys pictus* | 5 | 107 | .02 | .11 | .05 | .01 | .02 | .44 | .14 | .21 |
| *Perognathus californicus* | 9 | 165 | .07 | .07 | .01 | .02 | .01 | .21 | .53 | .09 |
| *parvus* | 6 | 142 | .29 | 0[2] | 0[2] | 0 | 0 | .08 | .38 | .24 |
| *Dipodomys panamintinus* | 8 | 211 | .01 | .06 | .12 | .11 | .11 | .02 | .30 | .25 |
| *Meriones unguiculatus* | 5 | 133 | .19 | .22 | .03 | 0[2] | .02 | .11 | .19 | .25 |
| *Gerbillus nanus* | 3 | 302 | .14 | 0[2] | 0[2] | .03 | 0 | .16 | .51 | .19 |
| *gerbillus* | 1 | 61 | .39 | .10 | .07 | .03 | 0 | .08 | .21 | .11 |
| *Allactaga elator* | 1 | 47 | .21 | .17 | .17 | 0 | 0 | .17 | .17 | .11 |

[1] Grooming generally occurs during mounting but was not scored separately.
[2] Noted in other series with anestrous females but of infrequent occurrence.

TABLE 18.—*Comparison of copulation patterns for selected rodents* (N=number of separate observation periods)

| Species | Number of mounts in N one series | | Mount durations (secs) | | Interval durations in series of mounts (secs) | | Series duration (mins and secs) | Special characteristics |
|---|---|---|---|---|---|---|---|---|
| | | | Range | Average | Range | Average | | |
| HETEROMYIDAE | | | | | | | | |
| *Perognathus californicus* | 5 | 5–14 | 1–5 | 2.3 | 1–16 | 4.7 | 70″–96″ | Male falls to one side at conclusion of mount with ejaculation |
| *Perognathus parvus* | 3 | 5–7 | 1–10 | 2.7 | 2–64 | 12 | 58″–82″ | Female and often male falls to one side at conclusion of mount with intromission as does *P. inornatus* |
| *Dipodomys panamintinus* | 3 | 2–3 | 30–513 | - | 1–20 | – | 8′12″–8′33″ | Long mount with terminal ejaculation |
| *nitratoides* | 1 | 3 | 60–180 | – | 30–120 | – | 8′30″ | Long mount with terminal ejaculation |
| GERBILLINAE | | | | | | | | |
| *Gerbillus nanus* | 1 | 1–10 | 1–3 | 1.5 | 6–20 | 14 | 60″–70″ | No special attributes |
| *Meriones unguiculatus* | 1 | 1–9 | .5–3.5 | 1.1 | 1–15 | 4.3 | 170″–200″ | No special attributes |

TABLE 19.—*Pairing tendencies of solitary rodents* (Pairing time varied from two weeks to three months)

| Species | Number of experiments | Cage size (sq.in.) | Sq. in. per Gm. | Sq. in. per animal | Pairing tendency | Remarks |
|---|---|---|---|---|---|---|
| *Heteromys anomalus* | 1 | 2304 | 26 | 1152 | Separate except for estrus | |
| *anomalus* | 1 | 6480 | 72 | 3240 | " | |
| *desmarestianus* | 2 | 2304 | 26 | 1152 | " | Wounding can result |
| *Liomys pictus* | 2 | 864 | 12 | 432 | " | " |
| | 6 | 1950 | 23.2 | 975 | " | " |
| | 2 | 6480 | 85 | 3240 | " | No wounding |
| *Perognathus parvus* | 2 | 550 | 21 | 275 | " | Wounding can result |
| | 2 | 6480 | 249 | 3240 | " | " |
| *inornatus* | 1 | 1950 | 75 | 975 | " | No wounding |
| *Microdipodops pallidus* | 2 | 5040 | 193 | 2520 | " | Wounding can result |
| | 3 | 6480 | 249 | 3240 | " | " |
| *Dipodomys merriami* | 1 | 5040 | 68 | 2520 | " | Male driven out at partus |
| | 1 | 1110 | 15 | 555 | " | " |
| *nitratoides* | 2 | 1110 | 15 | 2520 | " | " |
| | 3 | 5040 | 68 | 555 | " | " |
| *panamintinus* | 3 | 1110 | 5.5 | 555 | " | Some wounding may result |
| | 1 | 6480 | 41 | 3240 | " | No wounding |

TABLE 20.—*Pairing tendencies of tolerant to semitolerant rodents*

| Species | Number of experiments | Cage size (sq. in.) | Sq. in. per gm. | Sq. in. per animal | Pairing tendency | Remarks |
|---|---|---|---|---|---|---|
| *Peromyscus maniculatus* | 3 | 328 | 8 | 164 | Nest together | ♂ tolerated at partus |
| " | 3 | 776 | 18.5 | 388 | " | " |
| *crinitus* | 3 | 328 | 11 | 164 | " | No breeding |
| " | 1 | 772 | 25.8 | 388 | " | ♂ separate at partus |
| " | 2 | 1110 | 37 | 555 | " | " |
| *eremicus* | 2 | 328 | 8 | 164 | " | ♂ tolerated at partus |
| " | 2 | 776 | 18.5 | 388 | " | " |
| " | 1 | 1120 | 28 | 555 | " | " |
| *californicus* | 2 | 328 | 3.5 | 164 | " | " |
| " | 6 | 776 | 8.5 | 388 | " | " |
| *Meriones unguiculatus* | 2 | 550 | 5.5 | 275 | " | ♂ must be removed at partus |
| | 1 | 1728 | 17 | 864 | " | " |
| " | 1 | 2304 | 23 | 1152 | " | ♀ nests alone at partus |
| *hurrianae* | 4 | 180 | 1.8 | 90 | " | " |
| *Tatera indica* | 2 | 180 | 1.3 | 90 | " | " |
| " | 2 | 1728 | 12.3 | 864 | " | " |
| " | 1 | 2304 | 17 | 1152 | " | " |
| *Jaculus orientalis* | 1 | 2304 | 14.4 | 1152 | " | ♀ builds separate nest at partus |

TABLE 21.—*Pairing tolerance without the production of young*

| Species | Number of experiments | Cage size (sq. in.) | Sq. in. per gm. | Sq. in. per animal | Pairing tendency | Remarks |
|---|---|---|---|---|---|---|
| *Heteromys anomalus* | 1 | 180 | 2.0 | 90 | Nest together | No young |
| *Perognathus parvus* [1] | 2 | 550 | 21 | 275 | " | " |
| *Dipodomys nitratoides* [1] | 3 | 776 | 10 | 388 | " | " |
| *merriami* [1] | 3 | 1110 | 15 | 555 | " | " |
| *Meriones unguiculatus* [1] | 5 | 180 | 1.8 | 90 | " | " |
| *Gerbillus gerbillus* | 1 | 180 | 4.5 | 90 | " | " |
| " | 1 | 2304 | 58 | 1152 | " | " |
| *nanus* [1] | 2 | 550 | 21 | 275 | " | " |
| *Allactaga elator* | 2 | 1728 | 24 | 864 | " | " |
| " | 2 | 2304 | 32 | 1152 | Some tendency to nest separately | " |

[1] Species that were bred in either a greater space or by an encounter technique. Reproductive failure appears to result from either an inhibition of the female cycle or failure to implant.

TABLE 22.—*Colony growth experiments*

| Species | Founding number | Number of experiments | Number animals at termination | Cage size (Sq. in.) | Range of terminal density | | Ultimate cause of colony failure |
|---|---|---|---|---|---|---|---|
| | | | | | Sq. in./Gm. | Sq. in./animal | |
| *Peromyscus* | | | | | | | |
| a) *maniculatus* | 2 | 3 | 26, 19, 19 | 776 | 2.0–1.5 | 30–40 | Failure of ♀ cycle and some loss of young |
| *crinitus* | 2 | 1 | 8 | 776 | 6.5 | 97.5 | Failure of ♀ cycle (in part) |
| *eremicus* | 2 | 2 | 19, 10 | 776 | 1.5–3.8 | 76–30 | Failure of ♀ cycle with adult fighting |
| *californicus* | 2 | 6 | 11, 11, 7, 10, 4, 2 | 776 | 1.5–4.1 | 67.5–184.5 | Failure of ♀ estrous cycle |
| b) *crinitus* | 2 | 2 | 7, 6 | 1110 | 10.5–12.2 | 158–183 | Mortality by adult fighting plus a failure of the ♀ cycle |
| *eremicus* | 2 | 1 | 7 | 1110 | 7.9 | 158 | Mortality by adult fighting plus a failure of the ♀ cycle |
| *Dipodomys nitratoides* | 2 | 1 | 14 | 5040 | 10(9.9) | 360 | Extended fighting among the adults and abandonment of the young by the mother |
| *Tatera indica* | 6 | 1 | 11 | 1728 | 1.5 | 106 | Abandonment of the young by mothers; some fighting among males only |
| " | 8 | 1 | 24 | 1728 | .8 | 53 | |
| " | 17 | 1 | 23 | 1728 | .8 | 50 | |

TABLE 23.—*Relative differences in the thresholds of four behavioral pathologies associated with crowding (hypothetical)* (A=extended proximity of adult male causes female to stop estrous periods; B=in confinement the agonistic tendencies result in high mortalities; C=proximity of adults causes female to neglect or destroy young; D=proximity of adult male inhibits growth and maturation of young males)

| Type of social system | Thresholds for exhibition of pathological behavior | | | |
|---|---|---|---|---|
| | A | B | C | D |
| Social group | | | | |
| Communal (extended family group) | High | High | High | Intermediate |
| Pair unit only | High | Intermediate | Intermediate | Low |
| Loose social system | Intermediate | Intermediate | Low | Low |
| Solitary (dispersed) | Low | Low | Low | Low |

TABLE 24.—*Field and laboratory correlates for the three testing situations*

| Distribution in field | Encounter behavior (male-female) | | Pairing tendencies | Reproduction in confined populations |
|---|---|---|---|---|
| | Neutral arena | Territorial box | | |
| Communal | Contact-promoting | Brief defense; then contact-promoting | Sustained pair tolerance through parturition and rearing | Sustained with later curtailment |
| Pair association | Avoidance; then contact-promoting | Brief defense; then contact-promoting | Pairing up to parturition; female will tolerate male through rearing phase | Early curtailment |
| Solitary (dispersed) | Agonistic or avoidance | Agonistic and avoidance | Pairing only through estrus (normal); sustained pairing with no reproduction (pathological) | None, if area is small |

TABLE 25.—*Social trends for selected species*

| Social tendencies | HETEROMYIDAE | GERBILLINAE | CRICETIDAE | DIPODIDAE |
|---|---|---|---|---|
| Social group Communal Pair tolerance | | *Tatera indica* | *Peromyscus californicus*<br>*Peromyscus maniculatus*<br>*Peromyscus eremicus* | |
| Intermediate tolerance | *Heteromys anomalus* | *Meriones hurrianae*<br>*Meriones unguiculatus*<br>*Gerbillus gerbillus* | *Peromyscus crinitus* | *Jaculus orientalis*<br>*Allactaga elator* |
| Solitary (dispersed) | *Heteromys desmarestianus*<br>*Liomys pictus*<br>*Dipodomys panamintinus*<br>*Microdipodops pallidus*<br>*Perognathus californicus*<br>*Perognathus parvus*<br>*Dipodomys merriami*<br>*Dipodomys nitratoides* | *Gerbillus nanus* | | |